ORIGINAL ARTICLE

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Comparing infant and juvenile behavior in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): a preliminary study

Abstract The dichotomy between the two *Pan* species, the bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*) has been strongly emphasized until very recently. Given that most studies were primarily based on adult individuals, we shifted the "continuity versus discontinuity" discussion to the infant and juvenile stage. Our aim was to test quantitatively, some conflicting statements made in literature considering species differences between immature bonobos and chimpanzees. On one hand it is suggested that infant bonobos show retardation in motor and social development when compared with chimpanzees. Additionally it is expected that the weaning process is more traumatic to chimpanzee than bonobo infants. But on the other hand the development of behaviors is expected to be very similar in both species. We observed eight mother–infant pairs of each species in several European zoos. Our preliminary research partially confirms that immature chimpanzees seem spatially more independent, spending more time at a larger distance from their mother than immature bonobos. However, the other data do not seem to support the hypothesis that bonobo infants show retardation of motor or social development. The development of solitary play, environmental exploration, social play, non-copulatory mounts and aggressive interactions do not differ between the species. Bonobo infants in general even groom other group members more than chimpanzee infants. We also found that older bonobo infants have more nipple contact than same aged chimpanzees and that the weaning process seems to end later for bonobos than for immature chimpanzee. Additionally, although immature bonobos show in general more signs of distress, our data suggest that the weaning period itself is more traumatic for chimpanzees.

Keywords *Pan paniscus* · *Pan troglodytes* · Infant development · Inter-specific comparison · Captivity

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Introduction

For years the differences between bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) have been stressed. Presumably typical bonobo characteristics such as female dominance (Parish 1996), highly promiscuous sexual interactions (De Waal 1987; Kano 1992), low levels of aggression (Kuroda 1980; de Waal 1998), higher reconciliatory tendencies (de Waal 1998) and the apparent absence of infanticide (de Waal 1998; Kano 1998) all contrasted markedly with chimpanzee features. However, as research on bonobo socio-ecology and behavior gradually adds up, the bonobo-chimpanzee dichotomy needs to be reconsidered (Fruth et al. 1999; Doran et al. 2002; Hohmann and Fruth 2002; Vervaecke et al. 2003a). More recent research, revealing non-exclusive female dominance (Vervaecke et al. 2000; Stevens et al. 2001, 2003), severe aggression (Parish 1996; Vervaecke et al. 2000; Hohmann 2001; MDL personal observation), highly individual variation in reconciliatory tendencies (Palagi et al. 2004; B. Meuleman, personal communication), infant harassment (Vervaecke et al. 2003b; personal observation), and even possible infanticide by females (Hohmann and Fruth 2002), shifted nuances and suggests that there is considerable overlap in the adaptive potential of bonobo and chimpanzee behavior.

While generally research on adult bonobos has been the focus, information on infant and juvenile behavior is lagging behind. Hardly any quantitative data or results are reported when comparing the behavior of immature

bonobos and chimpanzees, and our understanding today remains primarily based on qualitative comparisons. So far only a few papers specifically reported on behavioral development in the wild (Kuroda 1989; Enomoto 1990; Hashimoto and Furuichi 1994). Even detailed information from immature captive animals, which can help to interpret the scarce data from field research, is rare (Johnson 1997; Weaver 1997). Additionally, the interpretations made are conflicting: on one hand it is suggested that bonobos are paedomorfic and show retardation in motor and social development when compared with chimpanzees (Kuroda 1989). On the other hand the similarities between the species' development seem to far outnumber the differences (Johnson 1997). Our aim is to make the first quantitative interspecific comparison using data on captive mother-reared individuals in order to test these conflicting statements.

First we will investigate the hypothesis that bonobos show a temporal retardation in motor and social skills (Kuroda 1989). Kuroda (1989, 2000) states that wild bonobos at 6 months of age are unable to move independently and that bonobo mobility remains poor until about 1-year old. One-year-old infants begin to play with other infants, but mothers keep them within hand reach (Kuroda 1989). Chimpanzees of the same age act much more independently as they often leave their mothers for more than 10 m (Kuroda 1989). Hence, we predict that, at least until 1 year of age, (1) bonobo infants will spend more time in ventral contact with their mother and (2) will spend less time not in contact with their mother when compared to chimpanzee infants. Additionally we predict that around 1 year of age (3) chimpanzee infants spend more time at a lager distance from their mother, (4) spend more time in solitary play and (5) environmental exploration, as well as more time socially interacting with other group members [(6) social play and (7) grooming] than bonobo infants.

Second we will test the hypothesis that the species have different weaning strategies. Although wild bonobo infants are weaned at approximately the same age as chimpanzees (Kuroda 1989), it has been suggested that the process may be more traumatic for chimpanzees than for bonobos: no weaning tantrums by bonobo juveniles have been reported in the wild (Kano 1992) and active rejection is not typically practiced by bonobo mothers (Kuroda 1989). In wild and captive semi-free ranging chimpanzees, infants are gradually weaned over a 2-year period and are considered completely weaned between 3.5 and 4.5 years of age (van Lawick-Goodall 1968; Clark 1977). We will test the predictions that chimpanzees and bonobos are weaned at approximately the same age as bonobos and that the weaning process is more traumatic to chimpanzees than to bonobos by inter-specifically comparing nipple contacts (8) and expression of distress (9).

Third we will investigate the hypothesis that the two species show differences in development of socio-sexual and aggressive behavior. Adult bonobos have highly promiscuous sexual interactions (de Waal 1987; Kano 1992) and are supposed to behave less aggressive (Kuroda 1980; de Waal 1998), than chimpanzees. Adult bonobos, in contrasts with chimpanzees, show a variety of non-copulatory sexual behaviors, which serve many social functions such as reducing tension among individuals, terminating agonistic interactions and forming and supporting new affiliative social relationships (de Waal 1987; Kano 1989, 1992; Hohmann and Fruth 2002). Although quantitative data on the performance of sexual behaviors of immature chimpanzees and bonobos are rare, the nature of behaviors expressed is relatively similar (Van Lawick-Goodall 1968; Hasegawa and Hiraiwa-Hasegawa 1983; de Plooij 1984; Kitamura 1989).

We will test the prediction that bonobo infants and juveniles are sexually more active and less aggressive than chimpanzees by comparing the development of sexual inspections (10), non-copulatory mounting (11) and severe aggressions (12).

Methods

Behavioral data collection

Study subjects include eight infants of each species, living in seven zoos (Tables 1, 2). Focal animal sampling on infants was conducted between January 2000 and December 2002 (for detailed information, see Table 1). Data were collected using instantaneous sampling (intervals of 15 s) (Altmann 1994). Each infant was sampled on average over five periods in 3 years. Infant age ranged from 5 to 56 months. An observation period consisted on average of six consecutive days. Each day five sessions of 30 min, randomly spread throughout the day, were carried out, resulting in 2.5 h of observation per day and 15 h per period. In total data were collected during 1,090 h. All mother–infant pairs were socially housed in multi-male multi-female social groups including animals of different age classes (except for the mother-infant pairs kept at Frankfurt Zoo, where group composition changed due to fission–fusion management and subgroups did not always contain an adult male). The bonobo group sizes ranged from 8 to 12 individuals; the chimpanzee group sizes ranged from 12 to 34 individuals. Given that our study was conducted during the course of 3 years, group compositions inevitably changed due to natural dynamics (Table 3).

All behaviors, as described below, were calculated as proportions of the observed time.

(1) Ventral contact: infant clings ventrally to the mother. (2) No contact: the infant does not touch the mother. (3) Distance far: proportion of no contact time that the infant spends at a distance of more than 5 m away from the mother. (4) Solitary play: climbing, swinging, rolling, and jumping, etc. including object play. (5) Exploration of the environment: touching, manipulating, licking, and sniffing the surrounding environment (this does not include objects). (6) Social

Table 1 Overview of observed bonobo infants and sampled periods

Infant	Sex	Date of birth	Data per observation period (year: month(s))	Infant age (months)	Institution
Zomi	F	28/1/1998	2000: 1, 5, 9; 2001:1, 5, 9; 2002:9	23, 27, 32, 35, 39, 43, 55	Planckendael
Zamba	M	16/4/1998	2000:1, 5, 9; 2001:1, 5, 9; 2002:9	21, 25, 29, 33, 36, 41, 52	Planckendael
Tarishi	M	17/9/1998	2000:1; 2001:1, 5, 9	16, 28, 32, 36	Apenheul
Kumbuka	F	9/7/1999	2000:1; 2001:1, 5, 9	6, 18, 22, 26	Apenheul
Liboso	F	17/1/1998	2000:1; 2001:1, 5, 9; 2002:9	24, 36, 40, 44, 56	Apenheul
Opala	F	8/4/1998	2000:3; 2001:3, 7, 11; 2002:11	23, 35, 39, 43, 54	Wuppertal
Ferry	F	25/9/1999	2000:3; 2001:3, 7, 11	5, 17, 21, 26	Frankfurt
Heri	M	23/3/2001	2001:7, 11	5, 10	Frankfurt

Wild Animal Park Planckendael, Mechelen, Belgium; Primate Park Apenheul, Apeldoorn, The Netherlands; Wuppertal Zoo, Elberfeld-Wuppertal, Germany; Zoo Frankfurt, Frankfurt am Main, Germany

Table 2 Overview of observed chimpanzee infants and sampled periods

Infant	Sex	Date of birth	Data per observation period (year: month(s))	Infant age (months)	Institution
Glafula	F	27/4/1999	2000: 2; 2001:2, 6, 10; 2002: 10	9, 21, 25, 30, 41	Amersfoort
Dwangko	M	22/4/1999	2000: 2; 2001: 2, 6, 10; 2002: 10	9, 21, 25, 29, 41	Amersfoort
Karibu-na	M	24/10/2000	2001: 6, 10; 2002: 10	7, 11, 23	Amersfoort
Liberius	M	20/1/1999	2000: 4; 2001: 3, 8, 12; 2002: 12	14, 26, 30, 34, 47	Edinburgh
Allity	F	27/12/1998	2000: 2; 2001: 2, 6, 10; 2002: 11	14, 26, 30, 34, 47	Burgers'
Galatea	F	24/2/1999	2000: 2; 2001: 2, 6, 11; 2002: 11	12, 24, 28, 32, 45	Burgers'
Zwala	F	16/4/1999	2000: 2; 2001: 2, 6, 10; 2002: 12	10, 22, 26, 30, 43	Burgers'
Raimee	F	15/5/1999	2001: 2, 6, 11; 2002: 11	21-25-29-42	Burgers'

Animal Park Amersfoort, Amersfoort, The Netherlands; Edinburgh Zoo, Edinburgh, United Kingdom; Burgers' Zoo, Arnhem, The Netherlands

Table 3 Sex and age distribution of the social groups

	Bonobo groups				Chimpanzee groups		
	PL	AP	WU	FR	AM	BU	ED
Adult male	2 (a:1)	4 (a:1, c:1)	3	2 (a:1)	3 (a:1)	4 (c:1)	3
Adult female	4 (a:1, c:1)	4 (a:2)	2	4	11	17 (a:1, c:2)	4
Adolescent male	1		1 (*:1)		1 (*:1)	2	2 (*:1)
Adolescent female	2 (c:1, d:1)	1 (*:1)		1 (c:1)		5	1
Juvenile/infant male	1	1 (a:1)	1 (a:1, b:1)	1 (b:1)	4 (b:2)	3 (a: 2, b: 2)	3 (*:1)
Juvenile/infant female	1	2	1	3 (*:2)	3 (*:2)	7 (a:2, *:1)	

PL: Wild animal park planckendael; *AP:* Primate park apenheul; *WU:* Wuppertal zoo; *FR:* Frankfurt zoo; *AM;* Animal park Amersfoort; *BU:* Burgers' zoo; *ED:* Edinburgh zoo
a: died during study; b: born during study; c: transfer out of group during study; d: transfer into group during study
*Changed to a higher age class during study

play: mouthing, wrestling, chasing individuals other than the mother; only those bouts initiated by the infant itself usually expressing a playface or relaxed facial expression were included. (7) Grooming: manipulating (e.g. licking, nibbling, picking with the fingers) an individual's body surface. Only grooming by the infants themselves was included.

(8) Nipple contact: the infant holds his mother's nipple in his mouth. (9) Distress: scratching (repeated movement of the hand or foot during which the fingertips are drawn across the hair), pouting, whimpering and tantrum. (10) Sexual inspections: inspecting (i.e. smelling, licking, touching) the genitals of a group member excluding the mother. (11) Non-copulatory mounts: all mounts or genito-genital contacts between the infant and the other group members, excluding the mother, which were initiated by the infant. (12) Aggression: all brusque movements, full speed pursuits and/or physical attacks often accompanied by high-pitched vocalizations; only interactions initiated by the infant with other group members, excluding the mother, were included.

Statistics

We conducted ANCOVAS, to investigate species differences; proportions of behaviors are the dependent variable, infant age is a covariate. We tested the main effects "species" and "infant sex" and focused on the interaction effect "species*infant age" and "species*sex infant". Because we sampled the infants several times during 3 years, a repeated measures design was used

with a random statement and the Kenwardroger option (Verbeke and Molenberghs 1997). The data were transformed to meet the requirements for parametric testing (Sokal and Rohlf 1981). All tests were two-tailed, performed in SAS (Version 8.0), and the alpha value was set at 0.05.

Results

The statistical results for the main effects species, infant age and infant sex and the significant interactions are included in Table 4.

From the 12 behaviors tested, only four showed a significant "species" effect: distance far (3), grooming (7), distress (9), and sexual inspections (10). Chimpanzee infants in general spend more time at a larger distance from their mother then bonobo infants [$F_{(1,25)} = 23.63$, $P < 0.0001$] (Fig. 1). They spend less time grooming other group members then bonobo infants [$F_{(1,11)} = 14.77$, $P < 0.01$] (Fig. 3) and they show in general less signs of distress compared to bonobo infants [$F_{(1,43)} = 9.87$, $P < 0.01$]. However, from 40 months of age onward chimpanzee infants start showing more signs of distress than bonobo infants (significant interaction species*infant age effect: $F_{(1,41)} = 5.03$, $P < 0.05$) (Fig. 4). Chimpanzee infants spend more time sexually inspecting other group members than bonobo infants [$F_{(1,25)} = 9.12$, $P < 0.01$]. This latter species difference is mainly due to a gender difference [significant interaction species*infant sex: $F_{(1,24)} = 5.40$, $P < 0.05$]. Chimpanzee male infants spend more time sexually inspecting other group members than male bonobo infants [$F_{(1,23)} = 14.30$, $P < 0.001$] (Fig. 5); the behavior does not differ between the female infants of the species [$F_{(1,16)} = 0.27$, NS].

For all other behaviors—ventral contact (1) (Fig. 1), no contact (2) (Fig. 2), solitary play (4) (Fig. 5), environmental exploration (5) (Fig. 6), social play (6) (Fig. 7), non-copulatory mounts (11) (Fig. 12) and aggression (12) (Fig. 13)—no significant species effect or

interaction effect with infant age or infant sex was found. Only for nipple contact did we find a significant interaction effect between "species" and "infant age" [$F_{(1,52)} = 4.31$, $P < 0.05$]. From 40 months of age infant bonobos have more nipple contact than chimpanzee infants (Fig. 4).

Discussion

Our aim was to test quantitatively, two conflicting statements made in literature considering species differences between immature bonobos and chimpanzees. On one hand it is suggested that bonobos show retardation in motor and social development when compared with chimpanzees (Kuroda 1989), but on the other hand the development of behaviors is expected to be very similar (Johnson 1997).

Our preliminary results, based on data from captivity, partially confirm the first hypothesis tested. Immature chimpanzees seem to spend more time at a larger distance from their mother than immature bonobos, but time spent in ventral contact and time spent not in contact with the mother do not differ between the species. Given the similarity in development of solitary play and environmental exploration, behaviors with a high-activity level, our results give reasons to doubt that bonobos show retardation of motor development. Initiating social play also does not differ between the species. Our results also indicate that immature bonobos groom more than immature chimpanzees. Grooming creates bonds that directly affect group cohesion and serves other important social functions such as stress reduction and reconciliation, which have been described as central features in bonobo society (de Waal 1989). Our results suggest that grooming may be a more important social tool for immature bonobos than chimpanzees. Hence, these results indicate that our study does not fully support the hypothesis that bonobo

Table 4 Results of the ANCOVA's

|	Behavior	Main effect species	Main effect infant age	Main effect infant sex	Significant interactions
1	Ventral contact	$F_{(1,13)} = 0.31$, $P = $ NS	$F_{(1,69)} = 28.70$, $P < 0.0001$	$F_{(1,13)} = 1.05$, $P = $ NS	None
2	No contact	$F_{(1,29)} = 0.25$, $P = $ NS	$F_{(1,43)} = 66.57$, $P < 0.0001$	$F_{(1,32)} = 3.98$, $P = $ NS	None
3	Distance	$F_{(1,25)} = 23.63$, $P < 0.0001$	$F_{(1,46)} = 84.72$, $P < 0.0001$	$F_{(1,27)} = 1.68$, $P = $ NS	None
4	Solitary play	$F_{(1,22)} = 0.04$, $P = $ NS	$F_{(1,46)} = 2.30$, $P = $ NS	$F_{(1,24)}$, $P = $ NS	None
5	Environmental exploration	$F_{(1,14)} = 0.17$, $P = $ NS	$F_{(1,71)} = 10.37$, $P < 0.01$	$F_{(1,14)} = 0.01$, $P = $ NS	None
6	Nipple contact	$F_{(1,68)} = 0.12$, $P = $ NS	$F_{(1,52)} = 9.79$, $P < 0.01$	$F_{(1,15)} = 0.17$, $P = $ NS	Species*Age Infant: $F_{(1,52)} = 4.31$, $P < 0.05$
7	Distress	$F_{(1,43)} = 9.87$, $P < 0.01$	$F_{(1,41)} = 10.04$, $P < 0.01$	$F_{(1,42)} = 4.24$, $P < 0.05$	Species*Age Infant: $F_{(1,41)} = 5.03$, $P < 0.05$
8	Social play	$F_{(1,33)} = 0.13$, $P = $ NS	$F_{(1,38)} = 32.51$, $P < 0.001$	$F_{(1,36)} = 0.11$, $P = $ NS	None
9	Grooming	$F_{(1,11)} = 14.77$, $P < 0.01$	$F_{(1,63)} = 41.61$, $P < 0.001$	$F_{(1,10)} = 0.05$, $P = $ NS	None
10	Sexual inspection	$F_{(1,25)} = 9.12$, $P < 0.01$	$F_{(1,52)} = 1.70$, $P = $ NS	$F_{(1,24)} = 1.36$, $P = $ NS	Species*Sex Infant: $F_{(1,24)} = 5.40$, $P < 0.05$
11	Non-copulatory mounts	$F_{(1,71)} = 3,45$, $P = $ NS	$F_{(1,71)} = 7.56$, $P < 0.01$	$F_{(1,71)} = 0$, $P = $ NS	None
12	Aggression	$F_{(1,25)} = 0.79$, $P = $ NS	$F_{(1,52)} = 14.56$, $P < 0.001$	$F_{(1,26)} = 1.40$, $P = $ NS	None
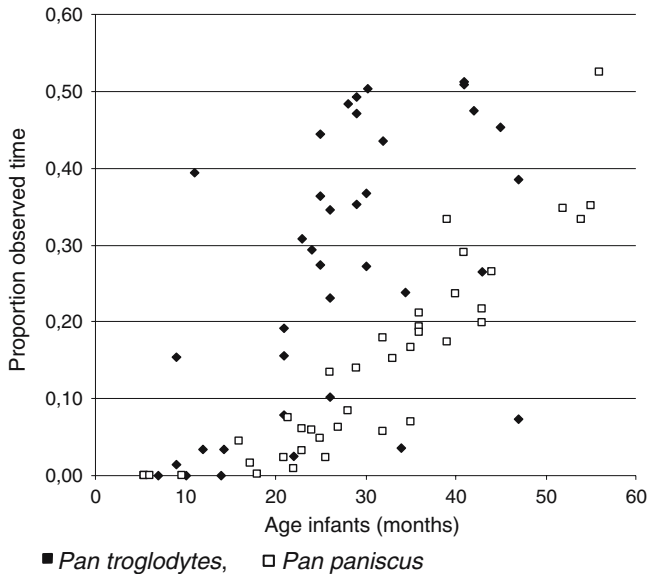
Fig. 1 Proportion of the observed time spent in no contact, which is spent in distance far (the infant is more than 5 m away from the mother) according to species and infant age
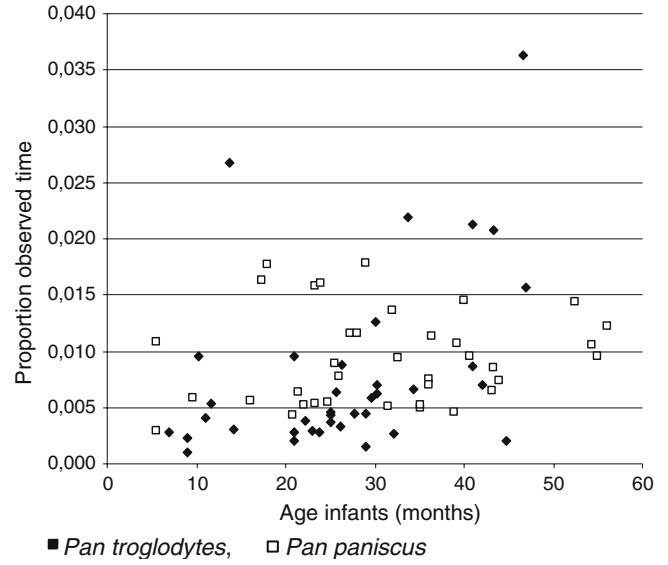

Fig. 3 Proportion of the observed time that the infants showed signs of distress according to species and infant age

infants show retardation of motor and social development.

The second hypothesis, that bonobo and chimpanzee infants are weaned at approximately the same age, seems not supported by our data. First, it is striking that nipple contact increases until about 3 years of age in both species, and even continues to increase beyond this age in bonobos. Second, the four juvenile bonobos, observed at an age older then 4 years, were still not fully weaned. In contrast, two out of four chimpanzee juveniles (observed at an age older then 3.5 years) were already in the

final stage of the weaning process and their mothers gave birth in the following months. The later weaning of bonobo infants in captivity is also reflected in the length of the interbirth intervals. Bonobo females in captivity have on average longer interbirth intervals than chimpanzee females (De Lathouwers and Van Elsacker 2005). In contrast with reports from the wild, active rejection by bonobo mothers does occur in captivity. Bonobo mothers even reject their infants more than chimpanzee mothers (De Lathouwers and Van Elsacker 2004), which may correspond with the general higher
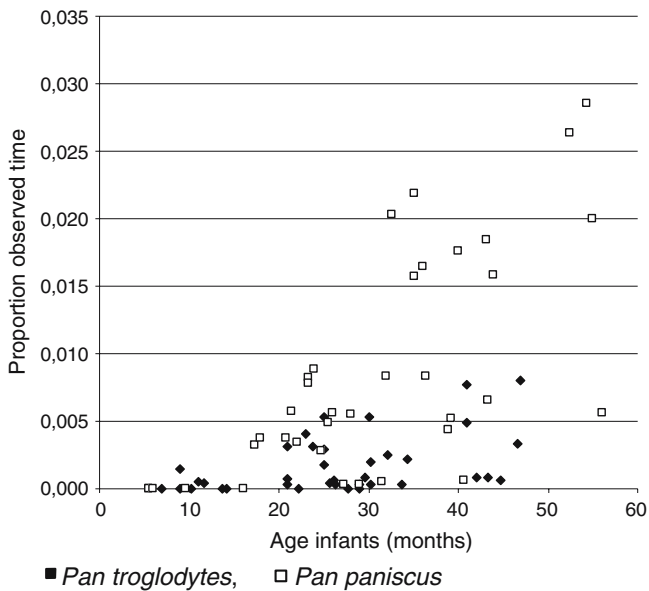

Fig. 2 Proportion of the observed time spent grooming by the infants according to species and infant age
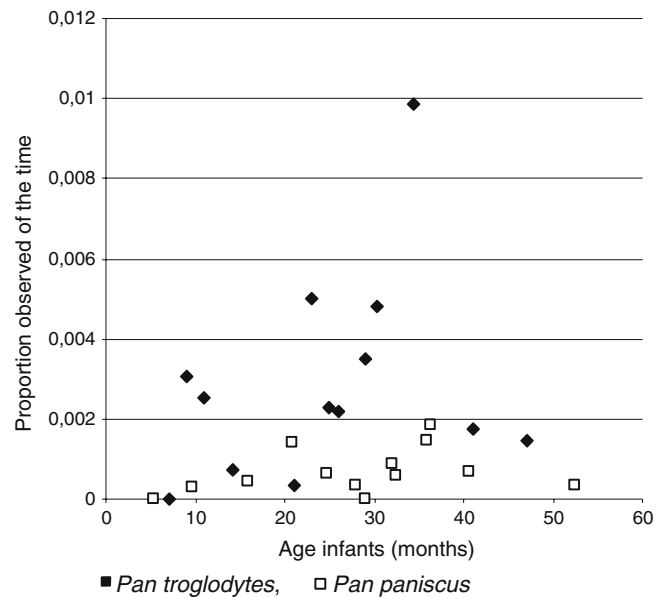

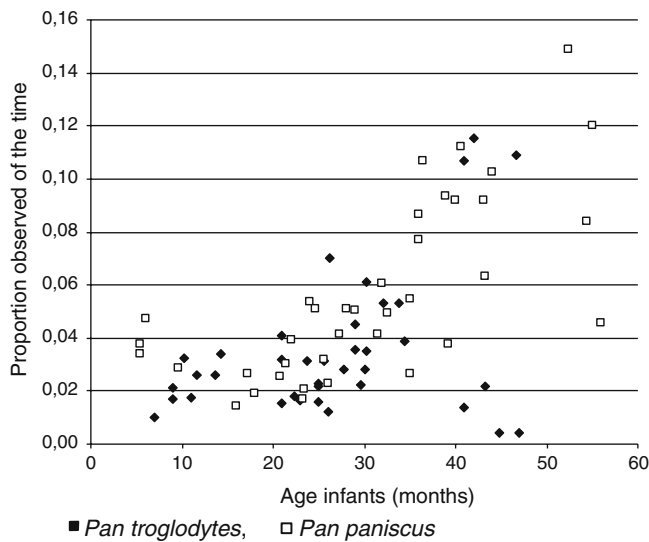**Fig. 4** Sexual inspections performed by male infants according infant age

Fig. 5 Proportion of the observed time spent in nipple contact according to species and infant age

expression of distress in bonobo infants. Juvenile chimpanzees however, show markedly more signs of distress from 35 months of age onward than bonobos, which corresponds with the onset of weaning.

Hence, our results seem to indicate that the weaning period itself seems more stressful for chimpanzee infants when being compared to the distress levels of younger un-weaned conspecifics and bonobos. More detailed analyses are needed to confirm whether the weaning bouts are indeed accompanied with simultaneous higher distress levels.

Finally, we tested the third prediction that bonobo infants are sexually more active and less aggressive than chimpanzee infants. We found no species difference regarding aggressive interactions initiated by the infants. This suggests that if species differences in aggression occur at the adult level, they will develop at a later stage than the developmental time frame investigated in this study. Contrary to the prediction regarding sexual activity we found that chimpanzee infants spend more time sexually inspecting other group members than bonobo infants, but this difference is more apparent when comparing only male infants. Our results indicate that differences in sexual behavior may already become apparent from an early developmental stage, in contrast with earlier studies (Hashimoto and Furuichi 1994), when gender differences are included. Further research is needed to investigate whether these early developmental differences are related to species differences in sexual competition between adult males.

The dichotomy between the two *Pan* species has been strongly emphasized until very recently. Given that most studies were primarily based on adult individuals, we shifted the "continuity versus discontinuity" discussion to the infant and juvenile stage. Our preliminary research reveals that the species indeed seem to resemble in their development of solitary play, environmental exploration, social play, initiated non-copulatory mounts and aggressive interactions, but it also emphasizes that species differences among infants and juveniles do occur. Bonobos and chimpanzees seem to differ in their development of spatial independence, nipple contact, grooming, expression of distress, and sexual inspections (Table 4). Development of behavior is influenced by a large number of variables. Sample size and other statistical restrictions did not allow us to correct for all, possibly influential, variables such as group size, age and experience of the mothers, presence of peers. Hence, we remain cautious with our conclusions. But we do hope that our findings may stimulate further investigation of species differences in development of behavior. It may prove to reveal striking differences and equalities that may aid us to understand species differences in association patterns, sociality, development of sexual behavior and temperament.

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