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Male Dominance Rank, Mating and Reproductive Success in Captive Bonobos (*Pan paniscus*)

R. Marvan[a, b]   J.M.G. Stevens[c]   A.D. Roeder[d]   I. Mazura[a, b]
M.W. Bruford[d]   J.R. de Ruiter[e]

[a]Department of Anthropology and Human Genetics, Faculty of Science, Charles University in Prague, and [b]European Centre for Medical Informatics, Statistics and Epidemiology – EuroMISE Centre, Prague, Czech Republic; [c]Group of Ethology, Department of Biology, University of Antwerp, Wilrijk, Belgium; [d]Cardiff School of Biosciences, Cardiff University, Cardiff, and [e]Department of Anthropology, University of Durham, Durham, UK

Abstract
In the recent past, application of DNA genotyping techniques has enabled researchers to more accurately test relationships between dominance rank (DR), mating success (MS) and reproductive success (RS). Paternity studies often reveal that reproductive outcome does not always correlate with male DR and/or MS and thus open room for discussion and interpretation of alternative reproductive tactics of both sexes. In this study, we analysed male DR, MS and RS in a group of bonobos at Twycross Zoo (UK). Genetic relationships were determined using 8 tetrameric microsatellite loci. Despite clear and asymmetric dominance relationships, analysed using normalised David's scores based on a dyadic index of dominance among the group's 3 mature males, we found that the most dominant male did not sire the most offspring. In fact, both infants conceived during the observation period were found to be sired by the lower-ranking males. Although the alpha male had almost exclusive mating access to one of the females during the time she was showing a maximal anogenital swelling, her infant was sired by the lowest-ranking male who mostly mated with her when outside the maximal swelling period. This result suggests that either sperm competition operates and/or ovulation is decoupled from the phase of maximal anogenital swelling which could allow greater female choice.
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Richard Marvan, Charles University in Prague
Faculty of Science, Department of Anthropology and
Human Genetics, Viničná 7
CZ–128 44 Praha 2 (Czech Republic)
Tel. +420 777 197 418, Fax +420 221 951 619
E-Mail r.marvan@seznam.cz

Introduction

For many years the number of copulations with ejaculation has been the only predictor of reproductive success (RS) in multi-male primate groups [Altmann, 1962; Suarez and Ackerman, 1971; Bernstein, 1981; Robinson, 1982; Fedigan, 1983; Cowlishaw and Dunbar, 1991]. During the last two decades, however, it has become possible to study RS by means of genetic markers [see review in de Ruiter, 2004]. As a result, the correlation between dominance rank (DR), mating success (MS) and RS can be determined, and (often complex) individual reproductive strategies can be analysed. The picture which has emerged is however still far from clear. This is partly due to contradictory results obtained both within and across taxa. In several studies, a positive correlation between male DR and RS has been found. However, there is a number of studies that have yielded no correlation, a weak or even negative correlation between DR and RS [see reviews in Ellis, 1995; Dixson, 1998]. Various factors may weaken the correlation between dominance and reproduction, such as number of males/females in a group, spatial distribution of females, sperm competition, kin relationships among the group members, rank position of a male's mother and female mate choice [Robinson, 1982; Fedigan, 1983; Cowlishaw and Dunbar, 1991; Takahata et al., 1999; Soltis et al., 2001].

At present, little is known about the relationship between DR, MS and RS in bonobos (*Pan paniscus*). In a study on wild bonobos, it was found that dominant males sire most of the offspring born within a community [Gerloff et al., 1999]. Dominant males are found to obtain a higher copulation frequency in some studies [Kano, 1996] but not in others [Furuichi and Hashimoto, 2004]. There is a number of species-specific characteristics which may cloud the correlation between DR and RS. First, the exact moment of ovulation in bonobos does not appear to be linked to the end of the maximal sex skin swelling phase. While the maximal swelling phase is closely linked to ovulation in common chimpanzees [Deschner et al., 2003; Klinkova et al., 2005], the relationship between maximal swellings and ovulation is less clear in bonobos where one third of the ovulations were found to occur outside the phase of maximal swelling, occasionally even up to 10 days after the onset of detumescence [Heistermann et al., 1996; Reichert et al., 2002]. Thus, dominant males may try to monopolize females when they have a maximal swelling even though this may not correspond to ovulation. Second, female bonobos can occupy high-ranking positions [Parish, 1996; Furuichi, 1997; Vervaecke et al., 2000, Stevens et al., in press]. Studies in other species in which females dominate males have shown that female choice occurs (*Lemur catta* [Pereira and Weiss, 1991], *Crocuta crocuta* [Engh et al., 2002]), therefore high female rank could indicate the potential for female choice in bonobos [Furuichi, 1992; Fruth et al., 1999]. Third, sperm competition may also be a very important evolutionary force in bonobos [Birkhead, 2000], since they have one of the largest testes sizes in relation to their body weight [Dixson and Anderson, 2004].

Here we report on a study of male MS and RS in a captive group of bonobos. One birth and two fertilization events occurred during the study period. Genetic tests were required to assess paternity of the offspring because there were multiple sexually mature males in the group. We describe the methods used to resolve the genetic relationships and relate dominance relationships among males with their respective observed mating behaviour and RS.

Table 1. Study group

Name	Acronym	Gender	Date of birth[2]	Age class	Place of birth	Parents (M × F)
Diatou	DT[1]	F	21/10/1977	adult	Stuttgart Zoo	MA × CA
Kakowet II	KA[1]	M	7/6/1980	adult	San Diego Zoo	KW × LI
Kichele	KC	F	19/4/1989	adult	Stuttgart Zoo	MA × DT
Jasongo	JS[1]	M	2/8/1990	adult	Wuppertal Zoo	MT × LL
Banya	BY[1]	F	1/2/1990	adult	Cologne Zoo	? × BN
Keke	KE[1]	M	2/1/1994	adult	Twycross Zoo	? × DT
Yasa	YS[1]	F	27/8/1997	juvenile	Twycross Zoo	? × DT
Kinshasa	KY[1]	F	19/10/2001	infant	Twycross Zoo	? × ?
Banbo	BB[1]	F	3/9/2002	infant	Twycross Zoo	? × BY
Luo	LU[1]	M	1/12/2002	infant	Twycross Zoo	? × DT

? = Parentage unknown.
[1] Hair samples obtained for genetic analyses.
[2] Data from Leus and van Puijenbroeck [2001].

Materials and Methods

Study Group and Observation Periods
At the time of study, the bonobo group at Twycross Zoo (Leicestershire, UK) comprised 3 sexually mature males (>7 years of age), 3 reproductively active females and 1 juvenile female. One of 3 infants (female) was born and 2 others (male and female) were conceived during the study period (table 1). Between October and December 2001 and in February 2002, 490 observation hours of behavioural data were gathered on 63 days.

Keepers found the dominant female, DT, carrying the first-born infant, female KY (table 1). However, there was doubt whether DT was the mother because she had had regular anogenital swellings prior to the birth of this infant. The lowest-ranking female BY, however, appeared weak and had heavy and irregular bleeding and a very irregular swelling cycle for several weeks after the birth [for more details, see Vervaecke et al., 2003]. The 2 other infants, male LU and female BB, were born to females DT and BY, respectively, approximately 8 months after the end of behavioural observations (table 1). With an average gestation period of 246 days [Thompson-Handler, 1990], they must have been sired during the observation period.

Behavioural Observations
Behavioural observations were only conducted when all members of the group were present. Observations usually started at 8.00 h and lasted until 17.00 h. During this time, observations were discontinued only when the animals were separated for cleaning or maintenance work (13.6% of possible total observation time). A combination of all occurrence sampling and focal animal sampling [Altmann, 1974] of the males was used to score male social and sexual behaviour.

Dominance Rank. The male hierarchy was based on the dyadic frequency of 'fleeing upon aggression' as a behavioural marker for dominance [Vervaecke et al., 2000]. We used normalised David's scores, based on a dyadic index of dominance (NDS-DDI values) [de Vries, 1998; Gammell et al., 2003; de Vries et al., 2006] to calculate dominance hierarchies for the males separately [Stevens et al., in press]. David's scores provide cardinal DRs, based on the overall success of individuals in conflicts [David, 1987; Gammell et al., 2003] and thus provide useful information on asymmetries in fighting ability. The normalised index varies from a minimum of 0 to a maximum of n – 1, where n is the number of animals in the group.

Mating Success. We included only copulations when calculating male MS, and discarded all non-copulatory mounts [Furuichi, 1992]. A sexual contact between an adult male and an adult female was only counted as copulation when the penis was erected and intromission of the penis as well as thrusting of the pelvis were observed. When two copulations followed each other in less than 5 min, these were counted as one copulation bout. To avoid a bias in MS towards males performing consecutive multiple mounts, we used the number of copulation bouts, rather than the number of copulations, as a measure of MS.

Swelling Cycles. The perineal swelling of every female was scored on a daily basis on a 3-rate scale, based on the firmness of swellings rather than on absolute size [Furuichi, 1987]: phase 0 = no swelling of the anogenital area; phase 1 = tumescent/detumescent phase, slight swelling of the anogenital area; phase 2 = maximal phase, full swelling of the anogenital area.

Genetic Samples

Hair samples were obtained in 2002 from all 9 relevant animals in the Twycross group (table 1; female KC had not reproduced at the time of the study, therefore she was not included in the genetic analysis); 12–15 plucked hairs with visible follicles were taken from each individual and placed in an unused paper envelope. All the samples were kept desiccated at room temperature for several weeks until DNA was extracted. Hairs that were not used were stored at –80°C [Vigilant, 1999]. A complication with assigning maternity of KY (see above) was resolved by genetic testing.

DNA Extraction

Two DNA extractions were performed per individual in order to produce adequate template DNA for PCRs. Six hairs were used for each DNA extraction. Approximately 2–3 mm of the follicular end of each hair was cut and placed in 200 µl of 5% Chelex suspension (Bio-Rad). After addition of 10 µl of proteinase K (10 mg/ml), the samples were incubated overnight at 56°C with constant mixing and then heated to 98°C for 10 min. Chelex beads were then precipitated by centrifugation at 11,000 g for 2 min. Two approximately 100-µl aliquots of Chelex-bead-free supernatant were transferred into new tubes. One tube from each extraction was kept at 4 or –20°C, and the second at –80°C. Before use, the products of the two extractions were pooled together to constitute a 1:1 extract. DNA concentrations for the extracts ranged from 53.8 to 172.3 ng/µl. For each PCR, 0.5–3 µl of the final extract was used as template.

Amplification of Microsatellite Loci

Every individual was genotyped at 8 human derived tetranucleotide microsatellite loci (*D1S550, D2S1326, D4S1627, D5S1457, D10S1432, D16S2624, D21S11, HUMFIBRA*) and the amelogenin XY-homologous locus [for details on primer sequences and expected sizes of PCR products, see Roeder et al., 2006]. All 9 loci were amplified in a single multiplex PCR and run on an ABI 3100 capillary semi-automated genetic analyser (Applied Biosystems) as described in Roeder et al. [2006]. For each locus, the products of at least 2 PCRs for each individual were genotyped separately. The local Southern algorithm was used for size standard assignment. The assigned sizes of the standard peaks were then checked manually. All allele designations were made using the program Genescan Analysis 3.5.1 (Applied Biosystems).

Kinship

Kinship between individuals was determined using the program GIMLET [Valiere, 2002]. Two input files were used for the calculations. The first file consisted of the genotypes of all individuals and the second consisted of birth year, sex and the classification as either a parent, an offspring or both for each individual. The maximum number of genetic incompatibilities was set at zero and the 'determine pair' of parents option was chosen.

Table 2. Frequencies of 'fleeing upon aggression' and the resulting dominance hierarchy positions based on the NDS and the DDI (y = –0.9107x + 2.8214; R^2 = 0.972)

Actors	Receivers			NDS-DDI	Male ranks
	KA	KE	JS		
KA	–	0	0	2.00	highest
KE	331	–	35	0.82	middle
JS	125	161	–	0.18	lowest

Table 3. Number of observed copulation bouts per dyad

Males	Females			
	DT[1]	BY[2]	KC[3]	sum
KA	61	14	10	85
KE[2]	0	168	31	199
JS[1]	57	9	25	91
Sum	118	191	66	375

[1] DT is mother of the infant LU, sired by the male JS.

[2] BY is mother of the infant BB, sired by the male KE.

[3] For the female KC only data on total mating success were analysed, since she did not reproduce during the study period. There were no additional data on male mating success during the conceiving of the infant KY by BY and KE.

Results

Dominance Relationships among the Males

Dominance relationships among the males were clearly developed and asymmetric. From 652 dominance-submission interactions in which one male fled from the other, we calculated the NDS, based on the DDI for the 3 males (table 2). The R^2 is close to 1, indicating that differences in NDS-DDI values are constant. KA had the highest NDS-DDI value because he never fled from any of the other males. The dominance relations between KE and JS were somewhat less clear, as both males had been observed to flee from one another. However, the relationships were asymmetric. In the dominance hierarchy, KA was the highest-ranking male followed by KE and finally JS.

Male MS

Altogether we observed 375 copulation bouts between the 3 mature males and the 3 mature females. The female DT never mated with her son KE, but she mated with both the other males with very similar frequency – of 118 copulation bouts involving DT, she mated 61 times with KA (52%) and 57 times with JS (48%). We

observed 191 copulation bouts involving BY. Of these, BY mated 168 times with KE (88%), 14 times with KA (7%), and 9 times with JS (5%). Finally, the female KC, who did not produce any offspring during our study, mated mostly with the middle-ranking male KE who is her half-brother (table 3). Overall, the middle-ranking male KE had the highest MS, followed by the lowest-ranking male JS, who still mated slightly more often than the highest-ranking male KA.

When we looked at sexual behaviour of the reproducing females DT and BY in more detail, we found the following patterns.

Female DT

We observed 2 complete sexual swelling cycles, and the end of another (in the beginning of the first observation period). Figure 1a shows the distribution of each male's copulation bouts in relation to the swelling cycle of DT.

It was conspicuous that both males focused on different phases of the swelling cycle. 85% of all copulation bouts of KA with DT were during phase 2, while only 24% of the copulation bouts with JS occurred during this phase. Conversely, of the 26 copulation bouts scored in phase 0 (no swelling), 4 (15%) were performed by KA and 22 (85%) by JS. In phase 1, 5 (22%) and 18 (78%) of the 23 copulation bouts were by KA and JS, respectively. Finally, in the maximal swelling phase KA obtained 52 copulation bouts (83%) versus 17 bouts (17%) for JS. Thus, it seems that KA focused on phase 2 and indeed obtained the highest proportion of copulations with DT in that phase, while JS copulated more frequently in the non-swollen phases 0 and 1.

When we restrict analyses to the period of 5 days before detumescence and the period of 5 days following detumescence (fig. 2a), we see that copulations are not distributed randomly (χ^2 = 35.40; d.f. = 1; p < 0.001). KA mated 33 times in the predetumescent period and only 4 times in the 5-day period following detumescence. JS however mated only 3 times in the period of 5 days before detumescence and 21 times in the postdetumescence period.
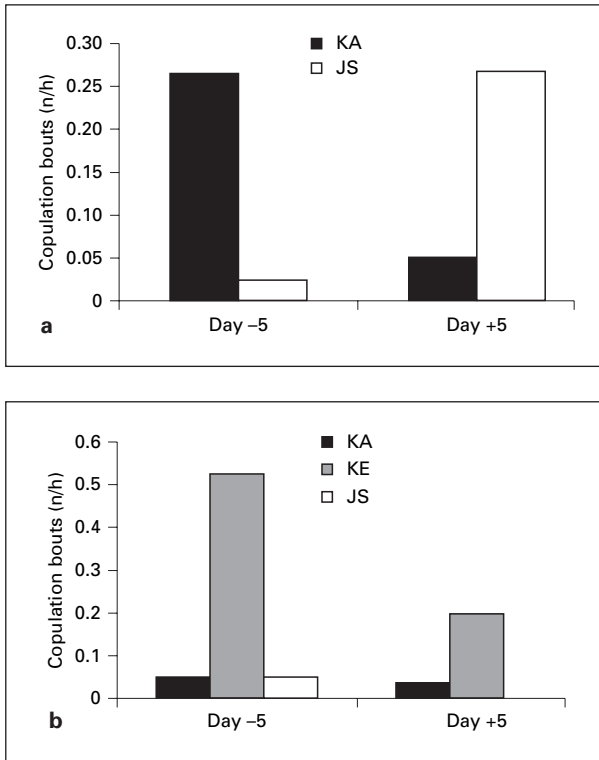
Female BY

During the first part of the observation period (October to December 2001), BY's swelling cycle was irregular and never reached full size (maximal phase), possibly because she had recently given birth to KY (see below). In contrast, during February 2002 she showed a maximal swelling almost continuously. The distinction between maximal and non-maximal phases was less clear and results mainly from the fact that days in which BY did not show any sign of swelling were very few. All 3 males copulated most frequently with BY in phase 2: 86% of KA's, 76% of KE's and 75% of JS's copulation bouts with BY were during this phase (fig. 1b).

In contrast to copulation bouts with DT, there was no marked difference between swelling phases regarding which male mated most frequently. In all three phases, KE obtained the highest proportion of copulation bouts with BY (phase 0: 75%; phase 1: 93%; phase 2: 83%). KA had 1 copulation bout in phase 0 (25%), 1 in phase 1 (2%), and 12 (8%) in phase 2, while JS had 0 copulation bouts in phase 0, 2 in phase 1 (5%) and 7 (5%) in phase 2.

When only 5 days before and after detumescence are taken into account, there was far less mating after detumescence in BY than there was in DT (fig. 2b). Even so, KE mated more than any of the other males in the 'postdetumescence window' (Wilcoxon matched pairs: Z = 1.60, p = 0.10).
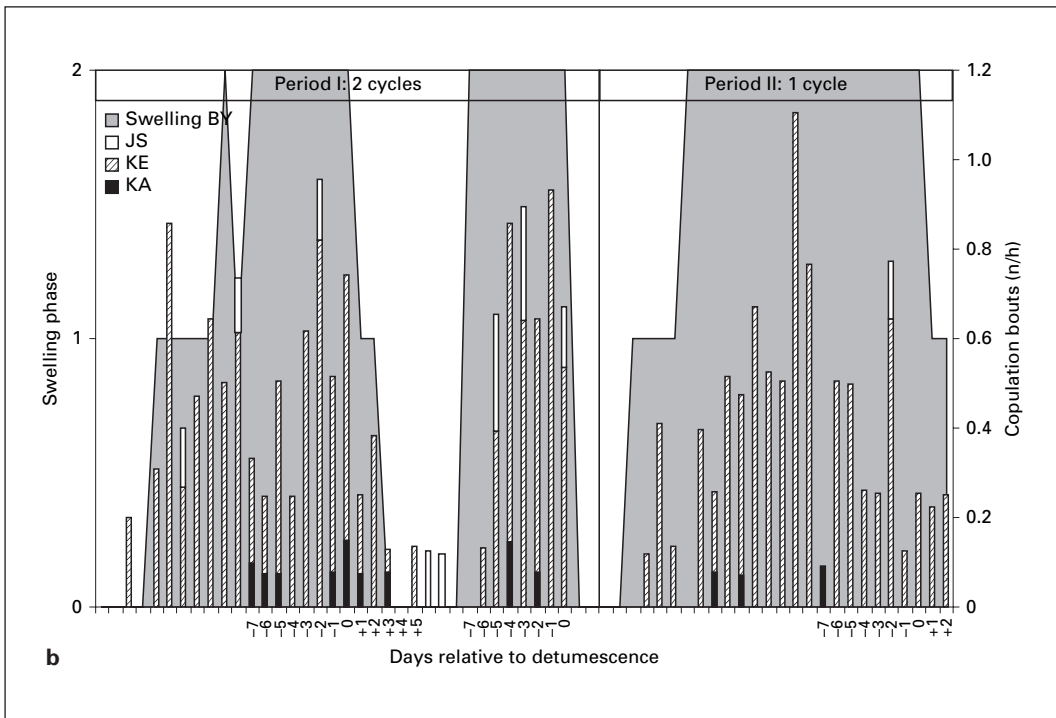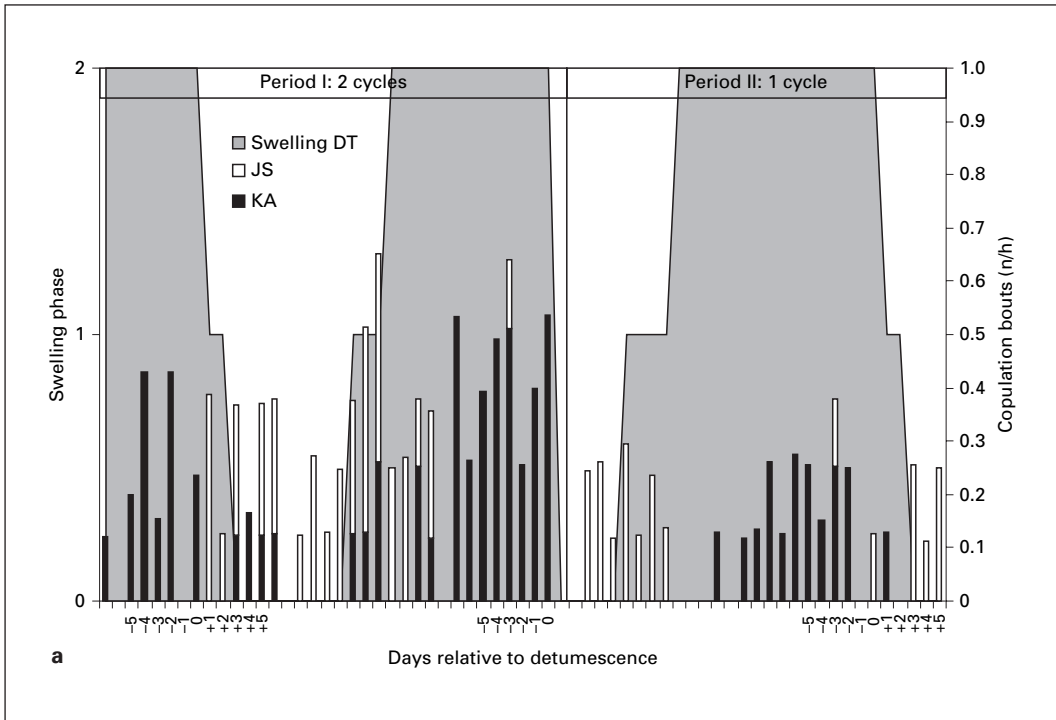
Fig. 2. Male mating frequencies with the females DT and BY, respectively, in the period of 5 days before including detumescence and in the period of 5 days after detumescence, corrected for the number of hours observed in each period. **a** The mating frequency of the males KA and JS with the female DT. **b** The mating frequency of the males KA, KE and JS with the female BY.

Reproductive Success

The genotypes of each individual are shown in table 4. Mother-infant pairs were known (except for the mother-KY pair) and are indicated in figure 3. In no instance was there a genetic mismatch between mother and offspring. The mother of KY was confirmed to be BY. For all offspring, only a single male could not be excluded as the sire. Based on the genotyping results, KA sired KE and YS. KE sired KY and BB, and JS sired LU (fig. 3).

Fig. 1. Numbers of male copulation bouts per hour per day with the females DT and BY, respectively, in relation to their anogenital swelling cycles (grey background). The perineal swellings were scored on a 3-rate scale (0 = no swelling; 1 = partial swelling; 2 = full swelling). **a** Number of copulation bouts per hour per day for the males KA (black) and JS (white) with the female DT. **b** Number of copulation bouts per hour per day for the males KA (black), KE (barred) and JS (white) with the female BY.

Table 4. Genotypes for the Twycross bonobos

Individual: Gender: Age class:	DT female adult	KA male adult	JS male adult	BY female adult	KE male adult	YS female juvenile	KY female infant	BB female infant	LU male infant
Amelogenin[1]	104/104	104/110	104/110	104/104	104/110	104/104	104/104	104/104	104/110
D1S550	158/162	146/158	158/166	162/162	146/158	146/158	158/162	146/162	162/166
D2S1326	249/265	245/269	241/257	245/257	245/265	245/265	257/265	245/265	241/265
D4S1627	194/206	214/214	218/218	194/210	206/214	206/214	194/214	194/206	194/218
D5S1457	118/122	126/134	118/122	118/126	118/126	122/134	118/118	118/126	118/122
D10S1432	167/175	167/171	171/175	167/167	167/175	167/167	167/167	167/167	171/175
D16S2624	118/118	118/118	118/118	122/122	118/118	118/118	118/122	118/122	118/118
D21S11	135/143	139/147	143/143	131/143	139/143	143/147	131/143	143/143	143/143
HUMFIBRA	181/207	189/289	185/215	189/207	181/289	207/289	181/189	181/189	207/215

[1] Females are 104/104 and males are 104/110.
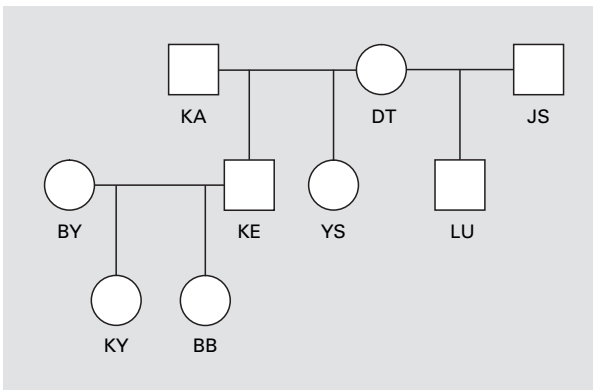
Fig. 3. Resulting bonobo pedigree based on the genetic determination of paternities and maternity. ○ = Female; □ = male.

Discussion

Even though the bonobo group size is admittedly small and systematic collection of samples for hormonal analysis was not possible due to management reasons, this study was the first to combine behavioural data on dominance relationships and MS with genetic data on RS in bonobos. Despite clear and asymmetric dominance relationships between the 3 males of the study group [see also Stevens et al., in press], there was no reproductive monopolization by the alpha male which is in agreement with earlier findings about DR and MS in this and other bonobo groups [Stevens, unpublished data]. The alpha male did not sire any of the offspring conceived after

the other two males (KE and JS) were sexually mature, although he had sired two offspring (KE and YS) when no rival males were present.

We could link MS to RS in 2 cases. In the first, the lowest-ranking male sired the offspring, although he was seen to mate more frequently in the non-swollen phases, while the alpha male mated most frequently when the female showed a maximal swelling. Thus the alpha male's DR was only correlated with selective MS [de Ruiter and van Hooff, 1993]. The sire also mated more frequently than the alpha male in the period of 5 days after detumescence.

In the second case, the middle-ranking male was seen to mate most frequently with the female throughout the entire swelling cycle, although he mainly copulated during the maximal swelling phase. In this case MS predicted RS. Although mating was far more frequent during the maximal swelling phase, the sire also mated more frequently than the other 2 males in the period of 5 days after detumescence. While previous studies have shown that ovulation can occur outside the period of maximal swelling in bonobos [Heistermann, 1996; Reichert et al., 2002], both the cases are the first examples that in a multi-male group mating after detumescence of the swelling could be a valuable reproductive tactic for lower-ranking males.

In general, dominance could be linked to MS in only 1 case and was not linked to RS in this study. Various factors can diminish the effects of dominance on reproduction. First, in bigger groups, many male competitors and/or simultaneously sexually receptive females are present, rendering it difficult for males to maintain exclusive access to females [Cowlishaw and Dunbar, 1991; Say et al., 2001]. Therefore, one would expect that in smaller groups the correlation between DR and fertilizations will be more pronounced. However, in our study group there were only 3 mature males and 3 females present and thus this factor seems unlikely. Second, wide spatial distribution of females is also believed to complicate monopolization by dominant males [Cowlishaw and Dunbar, 1991]. Obviously, this does not apply to our captive situation, where space was rather restricted and all the females were visible to all the males.

Female choice is a third factor which can influence the relationship between DR and MS. If females prefer mating with the dominant male, the relationship between dominance and MS will become stronger. However, female choice may be of only limited importance in some species where males can dominate females [Klinkova et al., 2005]. Conversely, when females are able to dominate males, female choice is expected to be relevant to male MS [Pereira and Weiss, 1991; Engh et al., 2002]. In captive bonobos, females can occupy high-ranking positions [Parish and de Waal, 2000], although there are also males that can outrank certain females [Vervaecke et al., 2000; Stevens et al., in press]. Thus, female choice may be expressed by dominant females. However, female mate choice has been inadequately studied in this species. The fact that all the 3 infants born or conceived during the observation period were sired by the lower-ranking males may indirectly suggest that females did not necessarily prefer the dominant male in our study group. However, more studies examining initiation of copulation are necessary.

A final factor which can disturb the correlations between DR, MS and RS is sperm competition. In none of the cases was there complete reproductive monopolization by 1 male during the maximal swelling phase, and all 3 males were observed to copulate with both the females when they were showing maximal swellings, which increases the potential for sperm competition [Packer, 1970; Birkhead and Kap-

peler, 2004]. When sperm of several males is present in the oviduct of a female mammal around the time of ovulation, sperm competition is most likely to occur through the raffle principle: the male with the largest number of mature sperm or with the most vital sperm is more likely to fertilise the egg [Gomendio et al., 1998; Dixson and Anderson, 2004].

Sperm quality in humans is related to age [Johnson et al., 1984; Bujan et al., 1988]. Although nothing is known about age-related differences in sperm quality in bonobos, it is possible that KA's sperm quality was reduced due to his age, even though at the time of the study he was still in his prime. Nevertheless, no testing has been done to determine whether he is still fertile.

Alternatively, it may be possible that sperm reserves of the dominant males are depleted by frequent ejaculation as in humans [Freund, 1963; Levin et al., 1986]. In a study of adolescent common chimpanzees, it was found that repeated ejaculation had an adverse effect on sperm quality; however, the effect was less pronounced than observed in humans [Marson et al., 1989]. Again, nothing is known about the effect of frequent ejaculation in bonobos or about its relation to age or social rank. Although our observation that the lowest-ranking male had far lower copulation frequencies on any given day than the other 2 higher-ranking males but still sired offspring supports the possibility that lower-ranking bonobo males may produce more sperm or sperm of a higher quality. This however, warrants further examination.

In conclusion, more information on this topic is needed and would best be accomplished by well-designed longitudinal interdisciplinary projects. In other words, research into relationships between male DR and mating behaviour that are accompanied by exact endocrine assessment of ovulation time and genetic determination of paternity appear to be the only promising practical approach for our deeper understanding of the evolutionary aspects of various primate reproductive tactics. Furthermore, better insights into the reproductive biology of this endangered great ape species will help it to be kept in more naturalistic groups while maintaining optimal genetic diversity.

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