

Determinants of Paternity Success in a Group of Captive Vervet Monkeys (*Chlorocebus aethiops sabaesus*)

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Abstract Paternity success of high-ranking primate males is affected by the number of males and the number of fertile females and their cycle synchrony. Female vervets in the wild show strong reproductive seasonality and do not advertise the ovulatory period with conspicuous signals or behavior. Because this makes it difficult for males to monopolize fertile females, it can be expected that male reproductive skew in this species is lower than in other cercopithecines living in multimale groups that advertise the ovulatory period. We assessed male reproductive success in a captive vervet group, initially consisting of 4 males and 12 unrelated females. Besides a general low reproductive skew, we predicted paternity success of the alpha males to be dependent on the overlap of synchronously fertile females, month into alpha male tenure, and housing conditions (the subjects were kept in a large park but had to be locked in a small indoor compartment during the winter months). Further, because the number of males reaching their prime increased over time, we predicted a decrease in reproductive success of the alpha male with increasing tenure length of the alpha male. To assess this we collected genetic samples from 27 of 32 offspring born into the group during 3 yr, using 7 polymorphic human microsatellite markers. Contrary to our predictions, reproductive success of the males occupying the alpha position during the study was among the highest found in cercopithecines, with the alpha males siring 78% of all offspring. The degree of overlapping fertile periods did not affect paternity success, nor did paternity success of the alpha male differ between the 2 housing conditions. Only the alpha male's tenure length had an effect. Alpha male reproductive success decreased over time, which we attribute to either a shift in female mate choice toward younger males or to increased competition among the males in the later stage of the alpha male's tenure. This study demonstrates the

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importance of assessing reproductive success of males throughout >1 season and should spawn more research into the role of female choice and postcopulatory mechanisms in this species.

Keywords Female choice · Male reproductive success · Paternity analysis · Vervets

Introduction

In primates with multimale social systems, paternity success of high-ranking males is usually affected not only by the number of males in a group, but also by the number of fertile females and their cycle synchrony (Ostner *et al.* 2008; van Noordwijk and van Schaik 2004; van Schaik *et al.* 2000), which in turn depends on the species' degree of reproductive seasonality. A high degree of female reproductive synchrony leads to a decline in reproductive skew in primates (Ostner *et al.* 2008). In many Old World primate species, females with multiple mating partners advertise timing of ovulation with signals (Clutton-Brock and Harvey 1976; Nunn 1999), such as swelling and/or reddening of the perineum, which also affects male potential for monopolization. Multiple explanations have been proposed for the evolution of conspicuous signals (Nunn 1999; Pagel 1994; Zinner *et al.* 2002). The existing evidence is most consistent with a female strategy to confuse paternity by mating with most group males to reduce the risk of infanticide by males but nevertheless allowing the highest-ranking males to monopolize most mating around the most probable days of ovulation (Nunn 1999; van Schaik *et al.* 2000; Zinner *et al.* 2002).

Among the cercopithecines that live in permanent multimale groups, vervets (*Chlorocebus aethiops*) are the only species in which females do not show any conspicuous signals (Hrdy and Whitten 1987; Melnick and Pearl 1987). Absent in vervets is also a well-defined period of increased sexual receptivity found in other primates that do not advertise timing of ovulation with sexual swellings. For example, hanuman langurs have a receptive period lasting several days to 2 weeks, during which females initiate copulations and males at least partly monopolize the females (Heistermann *et al.* 2001; Sommer *et al.* 1992). Genetic and hormonal data indicate that, although ovulation does occur during this receptive period, the exact timing of ovulation is not predictable for males, allowing lower-ranking males to sire a substantial portion of offspring (Heistermann *et al.* 2001). In contrast, the receptive period of vervets begins 2–3 mo before ovulation, and extends as long into the postconceptive period, without a pronounced increase in copulation frequency around days during which conception is most likely (Andelman 1987; Andelman *et al.* 1985). A prolonged period of receptivity is typical for primates, especially in catarrhines (van Schaik *et al.* 2000). But even within this primate taxon, vervets show an exceptionally long period of mating activity, and this, together with the absence of conspicuous signals, has led researchers to postulate that ovulation in vervets is concealed (Andelman 1987; Sillen-Tullberg and Moller 1993).

Reproductive seasonality not only leads to a higher degree of female reproductive synchrony, but also is related to the absence of conspicuous signals advertising ovulation (Nunn 1999; van Schaik *et al.* 1999). Among the primates with multimale social systems, only Barbary macaques display an exaggerated swelling despite

showing reproductive seasonality. In vervets, the females of a group typically conceive within 2–3 mo, which is exceptionally short given that other guenons have a reproductive season lasting 3–7 mo (Butynski 1988; Cords 2000). The high number of females conceiving within a relatively short period of time and concealed ovulation may explain why vervet males are not found to monopolize females by consorting them for extended periods (Andelman 1987; Cheney *et al.* 1988). Accordingly, the only long-term behavioral study of wild vervets focusing on mating behavior, published by Cheney *et al.* (1988) and Andelman (1987), shows that during a study of 3 groups lasting 7 yr there was no consistent relationship between male rank and mating success, with an average correlation coefficient between copulation success and male rank close to 0. However, researchers have not yet applied genetic methods to measure reproductive success of vervets.

The main aim of this study is to investigate the degree of reproductive skew in a captive vervet group. For this, we present genetic data from wild-caught vervets from St. Kitts and Nevis housed in an outdoor enclosure of the Centre de Primatologie, Strasbourg, over a 3-yr period. Based on a survey of available paternity data from primate species for which a comparable tight reproductive seasonality exists, we predict that the alpha male in a typical vervet group with 3–4 males will sire only 20–30% of all offspring (van Noordwijk and van Schaik 2004). If the alpha male would sire a much higher proportion of offspring than expected, this may indicate that either males have more information on the timing of ovulation or that female mate choice may play an important role in this species.

We also investigated the effects of 3 factors that are likely to affect paternity control of the alpha male. First, we looked into the relationship between the number of females conceiving within 30 d and paternity success of the alpha male. Although reproductive seasonality largely disappears in captivity owing to the protein-rich food supply throughout the year, there were time periods with very different numbers of ovulating females. If males have no information about probability of ovulation, we predict that they scramble for access to females, even when the number of fertile females is low. In this case, paternity success would be decided stochastically, regardless of the number of fertile females. However, if males have more information about ovulation and are able to monopolize matings, at least when only 1 or few females are fertile within a short time period, the priority of access model (Altmann 1962) would apply. Then, we predict that alpha male paternity success would be dependent on the number of overlapping conceptive periods. Second, we looked into the role of different housing conditions, which may influence the alpha male's ability to monopolize females. The large outdoor enclosure in Strasbourg is characterized by a ridge with a steep slope at 1 side that is almost completely covered by forest with a thick understory layer, providing individuals with the opportunity to spend time out of sight of the core group. But during the coldest winter months the group was locked into a heated indoor facility with access to a small outdoor enclosure to prevent frostbite of hands and tails. This setup allowed us to compare reproductive success of males during time periods in which they lived in more natural conditions, with periods during which space was limited. We assumed that the alpha male can exert his power more efficiently in the small enclosure, where there was little opportunity for lower ranking males to mate out of his sight. Finally, we investigated alpha male reproductive success throughout

his tenure. A single male held the alpha position over 30 mo until a younger male took over toward the end of this study. In vervets, sexual dimorphism is relatively small and females are able to reject male mating attempts (Andelman 1987; Cheney *et al.* 1988; Keddy 1986). We therefore predict that female mate choice plays a larger role than in other cercopithecines. Female preferences for the highest ranking male, which was the oldest group male, may shift toward younger males over time, as occurs in rhesus macaques (Berard 1999). A decrease of alpha male paternity success over time would reflect this shift in female preference.

Methods

Subjects and Housing Conditions

Nine adult females, 2 juvenile females, and 2 female infants were part of a free-ranging socially intact group of vervets living on St. Kitts and Nevis, West Indies, which was caught in November 2001. Females were kept separate from males at the Behavioral Science Foundation, Basseterre, St. Kitts, while awaiting transport to the Centre de Primatologie in Strasbourg in May 2002. Four males were captured in a different location than the females on St. Kitts and Nevis. *Post hoc* genetic analyses confirmed that none of the males was the offspring of a group female. The infants and juvenile females reached adulthood and gave birth to offspring during the study period. Group size and composition are within the range of groups in East Africa (Cheney *et al.* 1988; Struhsaker 1973), Southern Africa (Henzi and Lucas 1980), and the Caribbean (McGuire 1974).

In Strasbourg, we initially housed the group in a 12-m² indoor room with an adjacent 15-m² outdoor cage. These facilities are situated within a 0.5-ha park into which we released the vervets after 2 mo in quarantine. The 2-m high fence had electrified wires attached to it, which the vervets were trained to avoid during the 2-mo quarantine period (Weingrill *et al.* 2005). Because the vervets were not used to the cold winter conditions in Strasbourg, we kept them in the heated indoor compartment with access to the adjacent outdoor cage during the coldest winter months, December–April. The group was housed for 15 mo in the small enclosure and 22 mo in the park between May 2002 and May 2005 (Fig. 1).

All subjects underwent a medical check twice a year. The first check of the year took place in March or April shortly before their release back into the park and the second check in December after we trapped the group in the winter room. During the initial medical check, a veterinarian tattooed subjects and injected an individual transponder under their skin. The observers collecting behavioral data individually recognized all individuals without the aid of these markers. We determined the weight of individuals during each medical check, and obtained additional weight measurements for some individuals when they were captured to care for wounds. Veterinary staff estimated the age of the males at arrival based on appearance and tooth wear (GA: 9 yr; FR: 5 yr; MA 4 yr; LE: 3–4 yr). Vervet males from the Caribbean are considered adult at 4–5 yr (Horrocks 1986; McGuire 1974). In captivity, subadult vervet males at the age of 3 yr are able to fertilize females (Bramblett *et al.* 1975). Therefore, we regarded all 4 males as potential sires from the start of the study.

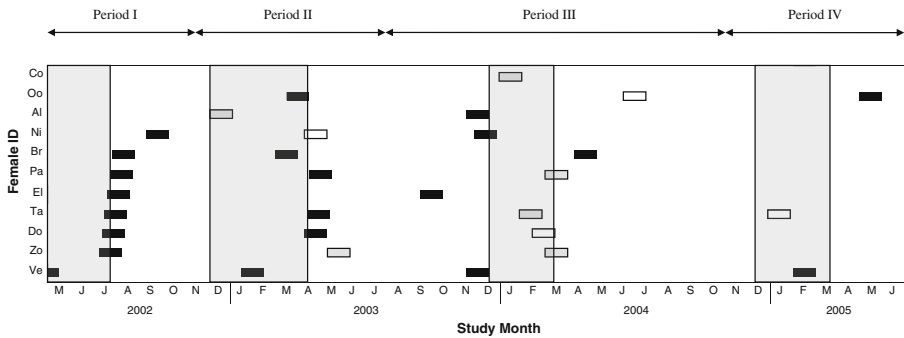


Fig. 1 Fertile periods, estimated on the basis of the date of birth, of females that gave birth during the study. Black bars indicate paternity of alpha male, gray bars paternity of lower-ranking males, and white bars unknown paternity because of lack of genetic data. Time periods during which the subjects were kept in the small enclosure are marked with a gray background. The study is divided further into 4 periods corresponding to the clusters of conception. Period IV coincides with tenure of the new alpha male MA.

Collection of Behavioral Data

Students conducting various research projects between June 2002 and September 2004 recorded behavioral observations, including data on agonistic interactions and mounts. During this time period, they observed the vervet group for 3–8 h on 473 d. Because of topology and thick vegetation in the park, we could not use a focal animal sampling method. Therefore, we used data collected *ad libitum* to generate the distribution of mounts among the males of different rank and to describe agonistic interactions between the males. Because in most cases it was not possible to verify if copulations resulted in ejaculation, the numbers of mounts in our analysis include complete and uncompleted copulations.

We determined the rank of individual males by creating an interaction matrix based on displacement events involving submissive displays during dyadic interaction. Although we collected no systematic data after October 2004, observers still working regularly with the group estimated the rank position of the remaining 3 males. To maximize interobserver reliability, T. Weingrill trained all observers to collect data. Changes in rank and weight of the males over the study period May 2002–May 2005 are provided in Fig. 2. According to the interaction matrix, the youngest male LE was already the second ranking male during the first year of the study although he was still much smaller than the other males. He approached the weight of the other males in summer 2003.

LE stopped showing submissive behavior toward the top-ranking male GA in the third year (period III) of the study. In October 2004 we observed severe conflicts, one of which ended with LE climbing over the electric fence to avoid the alpha male. A few days later we reintroduced LE to the group, but he left the park again after a few hours, after which we decided not to return him to the group. Group size increased from 17 to 38 between May 2002 and December 2004. Therefore, we had to separate 10 individuals, including one of the founder females, from the group because the indoor enclosure was too small to accommodate the high number of subjects. We later transferred them to a French zoo together with LE. In December 2004, most of the remaining adult females received a contraceptive implant to keep group size stable.

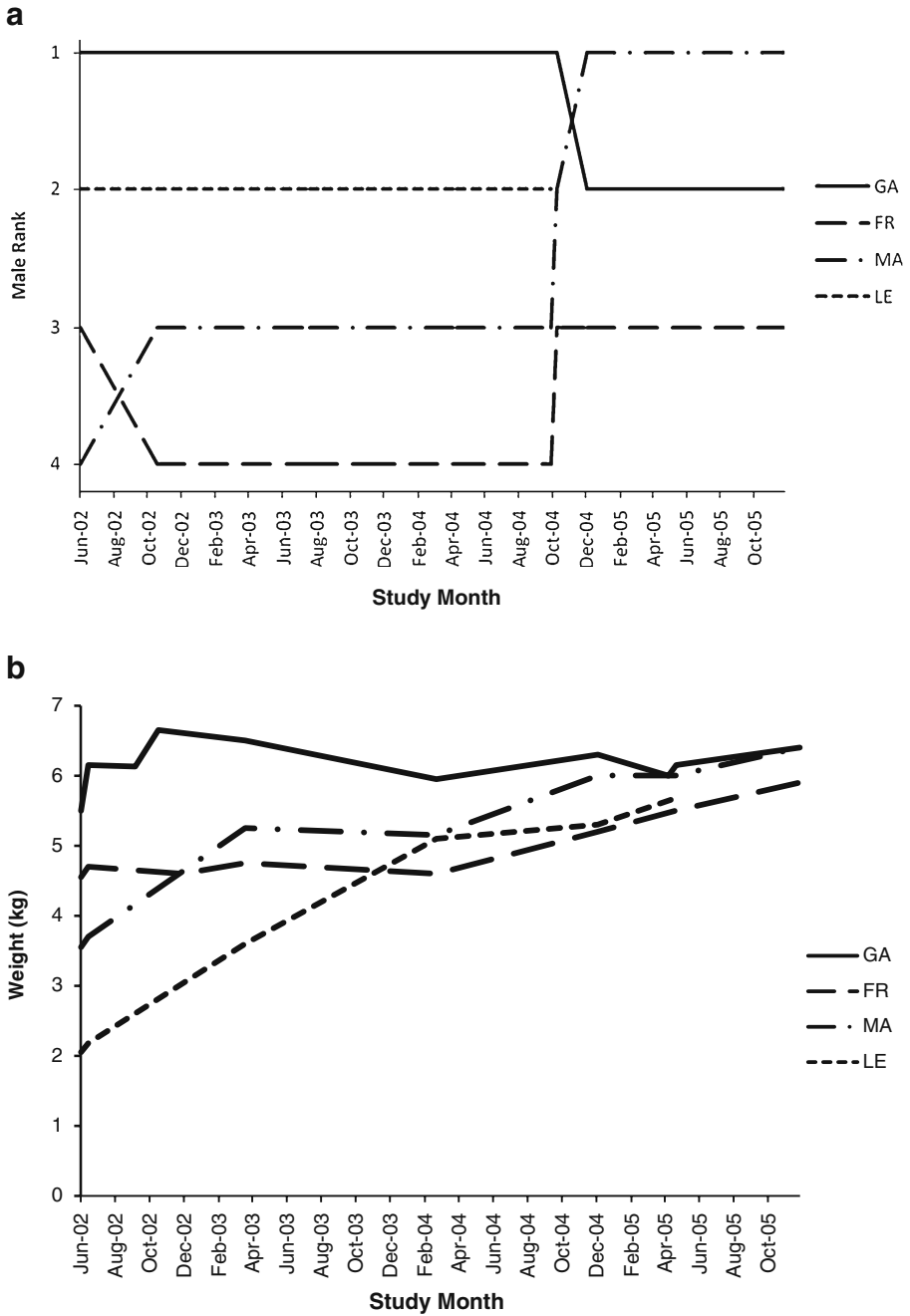


Fig. 2 Male rank (a) and male weight (b) throughout the study period, including the last health inspection in October 2005. LE was removed from the troop in October 2004, but weight was recorded until April 2005.

Number of Overlapping Fertile Periods and Study Periods

Mean gestation length in vervets in captivity is between 163 (Bramblett *et al.* 1975; Johnson *et al.* 1973) and 165 d (Rowell 1970), and we assumed a gestation length of 164 d to estimate conception dates. Female vervets do not show proceptive behavior and increased mating activity around days on which ovulation is most likely, and the receptive period lasts over 3 mo in wild vervets (Andelman 1987). Therefore, we defined a more fertile period within this receptive period as lasting 30 d, in which the assumed day of conception is d 16. This 30-d period should account for variance in gestation length and indicates a period during which conceptions can occur. To examine the effect of overlapping fertile periods on paternity success of the dominant male, we calculated for each fertile period the number of overlapping fertile periods with other females, which ranged from 0 to 5 (Fig. 1).

Because we introduced males to the females only after arrival in Strasbourg, we found a clustering of conceptions comparable to seasonality in the wild only in the first few months of the study. Seasonal breeding was not apparent in captivity, but we could distinguish between 3 distinct reproductive clusters of births during the tenure of alpha male GA and an additional one during the tenure of his successor MA. Therefore, instead of splitting the study period into time periods of equal length, we defined 4 time periods corresponding with the clusters of conception (Fig. 1).

Paternity Assessment

During the medical checkups, 5 ml of blood was drawn from all group members into Vacutainer tubes containing EDTA. Tissue samples were available from 3 of the 8 infants that were stillborn or died soon after birth. We could not find the remains of 5 infants in the park. We stored the samples in a freezer and shipped them frozen to the University of Zurich. We conducted DNA extractions and polymerase chain reaction (PCR) setups in dedicated laboratories to avoid human or cross-contamination of samples. Using whole blood, we performed DNA extractions with the Qiagen blood kit (Qiagen, Hilden), according to the manufacturer's instructions. We genotyped all subjects for 7 human microsatellite loci (Table I), which Newman *et al.* (2002) had previously shown to be polymorphic in vervets. We conducted PCR for each locus individually on a DNAEngine Dyad (Bio-Rad), and diluted PCR products 20- to 50-fold before analyzing them on an ABI 3730xl capillary sequencer (Applied Biosystems). To measure the size of the fragments and to assign genotypes, we used GeneMapper, version 4.0. This was followed by assessing the potential of human cross-contamination by performing separate extracts for 15% of the samples, and by comparison of genotypes of the reextracts with those obtained during the initial extraction. The replicate samples did not reveal any potential for human contamination.

We found all 7 microsatellite loci to be polymorphic, with a mean number of alleles per locus of 5.43 (Table I). All loci were in Hardy-Weinberg equilibrium, and we detected no null alleles. The combined power of all loci to exclude a randomly selected unrelated candidate parent was 0.989. The probability of identity was 6.3×10^{-7} and 2.7×10^{-3} for 2 unrelated individuals and siblings, respectively, suggesting that there was sufficient statistical power to exclude nonparents.

Table 1 Locus characteristics for paternity analysis

Locus	N	N_a	N_e	I	H_O	H_E
D3S3591	44	5	2.95	1.19	0.75	0.66
D2S144	43	7	4.74	1.71	0.86	0.79
D1S518	43	3	2.55	0.99	0.70	0.61
D18S72	42	7	4.59	1.66	0.86	0.78
D15S108	44	6	3.48	1.39	0.82	0.71
D11S1902	44	5	2.94	1.19	0.75	0.66
D5S1466	43	5	3.85	1.47	0.79	0.74
Average		5.43	3.59	1.37	0.79	0.71
(SE)		(0.53)	(0.32)	(0.10)	(0.02)	(0.03)

N = number of subjects; N_a = number of different alleles; N_e = number of effective alleles, I = Shannon's Information Index, H_O = observed heterozygosity; H_E = expected heterozygosity; (SE) = standard error

We used CERVUS, version 2.0 (Marshall *et al.* 1998), to assign paternities and calculate basic loci characteristics such as expected and observed heterozygosity, polymorphic information content, and the occurrence of null alleles. CERVUS employs a simulation approach to define a Δ -statistic based on population allele frequencies and resolves paternities between the 2 males with the highest LOD scores (Meagher 1986) with a known level of statistical confidence based on this statistic (Marshall *et al.* 1998). The input parameters required are the number and proportion of candidate sires sampled, the proportion of loci typed, and the genotyping error rate. We set the number of candidate sires to 4, and other parameters for the CERVUS simulation file to 0.984 for the proportion of loci typed and the observed typing error rate to 2%. We assessed paternities at a 95% confidence level.

Data Analysis

For all births for which paternity could be determined genetically ($N=27$), we assessed the potential effects on alpha male paternity, i.e., whether or not the alpha male sired the offspring, of number of receptive females, housing conditions, and time into an alpha male's tenure at the estimated time of conception. Initially, we fitted a generalized linear mixed model (GLMM) with a binomial error distribution using the `glmer` function in R 2.10.1 (R Development Core Team 2009). As fixed effects, we coded the number of cycling females, housing condition, and time into tenure, whereas we incorporated alpha male identity as a random factor. However, because inclusion of the random factor led to an increase in AIC value (Δ AIC=2.00) without accounting for a significantly larger amount of variance in comparison to a binomial general linear model (log-likelihood ratio= 3.17×10^{-9} , $P_{\text{MCMC}}=0.37$), we dropped this term (note that parameter estimates and significance values of the fixed effects were identical in the GLMM and GLM). Our results stem from the binomial GLM built with R's `glm` function. Further, we calculated the Spearman's correlation coefficient between male rank and the number of offspring sired during the tenure of male GA. All statistical tests were 2-tailed and the α -level was set at 5% for all analyses.

Results

In total, we observed 146 mounts between June 2002 and September 2004. Throughout his tenure, the highest ranking male, GA, mounted females most often (52 copulations), followed by LE (47), FR (28), and MA (19). The proportion of copulations of the alpha male decreased from 61% in period I (33 of 54 observed matings) to 39% in period II (7 of 17 observed matings), and dropped to only 17% in the last period of his tenure (12 of 75 matings). This was due mainly to LE mounting most often ($N=41$) in the third time period. The number of mounts during periods when females were likely to be fertile was too low and missing for too many time periods for a more detailed statistical analysis. We observed only 17 matings during the estimated fertile periods of females. These matings were more evenly distributed among the males between period I (GA: 1, MA: 1), period II (GA: 2, FR: 2, LE: 2), and period III (GA: 2, FR: 3, LE: 3, MA: 1).

We could assign a single male as the sire at the 95% confidence level to each of the offspring ($N=27$). Further, we could exclude all other males at ≥ 2 loci (Table II). Altogether, GA sired 19 (76%) of all infants for which genetic data were available during his tenure as alpha male (period I–III). The 3 other males together sired 6 infants, of which 3 were offspring of LE, 2 of MA and 1 of FR. Over GA's tenure, the correlation between male rank and reproductive success was significant (Spearman rank correlation: $r_s=1.00$, $p<0.05$). After MA became the top-ranking male in December 2004, he sired the 2 offspring for which genetic data were available (period IV).

Alpha male paternity success was not affected by the number of cycling females or housing condition, but dropped significantly with increasing time into a male's tenure at the estimated time of conception (Table III). Figure 3 indicates the estimated dates of the 27 conceptions that resulted in offspring whose paternity could be determined genetically. It shows mean empirical probabilities of alpha male paternity over the 4 consecutive receptive periods, along with their standard errors, to illustrate graphically the fit of the logistic curve (Crawley 2007).

Discussion

Dominance rank and paternity success correlate strongly in this study. A high proportion of offspring (76%) was sired by GA during the 30 mo in which he was the alpha male of the group. His successor fathered both infants for which genetic data were available in the last 8 mo of the study. Only alpha male tenure had a significant effect on the reproductive success of the highest ranking male in the group. During all periods of this study, the alpha male sired most offspring, but the proportion of offspring sired by GA decreased from 100% in the first period of his tenure to 56% in the third period. Even if period I is excluded, because ≥ 1 male could not be considered fully adult at the beginning of this study and GA therefore may have had less competition, he sired 65% of offspring for which genetic data were available in periods II and III. Only mandrills (75%, with 6 males present in the group), stump-tail macaques (95%, 2 males), savannah baboons (81%, 5 males), and long-tailed macaques (67% and 75.3%, 5 males) showed similar high proportions of

Table II Infants born during the study period and paternity data of offspring for which genetic samples were available

Date of birth	Remarks	Assigned sire	Loci typed	Loci compared	Loci mismatch	LOD score	Δ
October 11, 2002		GA	7	6	1	0.13	0.13
January 1, 2003		GA	7	7	0	2.48	1.86
January 3, 2003		GA	7	7	0	2.78	2.11
January 6, 2003		GA	7	7	0	2.9	2.60
January 13, 2003		GA	7	7	0	2.31	2.31
January 17, 2003		GA	7	4	0	0.40	0.40
January 22, 2003	Stillborn	GA	7	7	0	3.90	2.94
March 7, 2003	Died after 3 d	GA	7	7	0	2.52	1.60
June 1, 2003		FR	7	7	0	4.67	4.67
July 15, 2003		GA	7	7	0	2.38	2.38
August 24, 2003		GA	7	7	0	3.99	2.99
September 16, 2003		GA	7	7	0	3.52	3.52
October 2, 2003	Twin, died after 1 d	No samples					
October 2, 2003	Twin, died after 3 d	No samples					
October 3, 2003		GA	7	7	0	2.31	2.31
October 8, 2003		GA	7	7	0	4.41	4.41
October 13, 2003		GA	7	7	0	4.35	4.35
November 1, 2003		MA	7	7	0	4.18	4.18
March 15, 2004		GA	7	7	0	3.44	3.44
May 15, 2004		GA	7	7	0	3.97	3.97
May 15, 2004		GA	7	7	0	4.00	4.00
May 24, 2004		GA	7	7	0	3.63	3.63
June 27, 2004		LE	7	7	0	4.28	4.28
July 25, 2004		LE	7	7	0	4.32	4.32
August 12, 2004	Stillborn	No samples					
August 27, 2004		MA	7	7	0	3.49	3.49
August 28, 2004		LE	7	7	0	4.69	4.69
October 6, 2004	Stillborn	GA	7	7	0	3.49	3.49
December 13, 2004	Died	No samples					
June 27, 2005	Died	No samples					
July 31, 2005		MA	7	7	0	3.91	3.87
October 23, 2005		MA	7	7	0	4.08	4.03

offspring sired by alpha males (Altmann *et al.* 1996; Bauers and Hearn 1994; de Ruiter *et al.* 1994; Dixson *et al.* 1993; Engelhardt *et al.* 2006). In all other cercopithecines living in multimale social systems, for which genetic data collected in the wild or in captivity are available, paternity concentration was reported to be lower (Clarke *et al.* 2009; Ostner *et al.* 2008; van Noordwijk and van Schaik 2004). Although the number of males in our study was relatively low, the high paternity success of alpha males in this group is surprising given that ovulation in this species is assumed to be concealed.

Table III Parameter estimates, standard errors, z values, and statistical significance of the three factors investigated for their effect on alpha male paternity

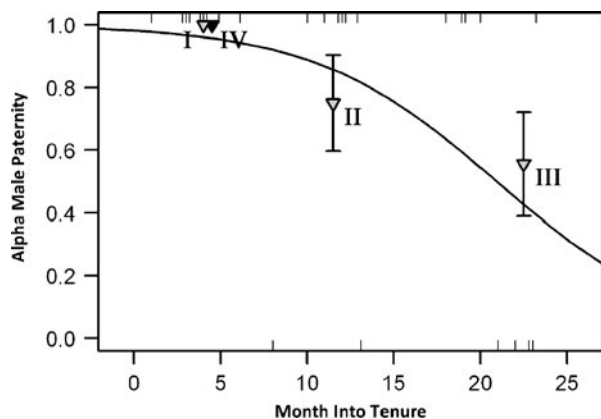
Model coefficients	Estimate	SE	z value	p
Intercept	2.95	2.12	1.40	0.163
n cycling females	0.97	0.67	1.45	0.148
Housing condition	-0.31	1.33	-0.24	0.814
Time into tenure	-0.25	0.12	-2.07	0.038

Overall significance of GLM: $\chi_{(1,23)}^2 = 7.90$, $p < 0.005$, AIC=26.01

SE = standard error

In the wild, vervets have a pronounced reproductive seasonality, and the absence of seasonality in this study may have only partly contributed to the high paternity success of the alpha male. Females in our study did not have contact with males until shortly before they arrived in Strasbourg, which artificially created a situation resembling a mating season with 6 females conceiving within a short period of time in the first months of the study. Later in the study, owing to similar interbirth intervals of the females, conceptions remained clustered, but there were periods with very different number of females conceiving within 30 d, ranging from 1 to 6. Thus, although no reproductive seasonality occurs in captive vervets, we expected to find a negative relationship between paternity success of the alpha male and the number of females conceiving within 30 d. However, the number of females conceiving did not have a significant effect on paternity success in our study. The alpha male sired all offspring in the first months of the study when ≤ 6 fertile periods of females overlapped and the 3 infants sired by lower-ranking males in 2002 and 2003 were conceived unexpectedly during times when only 1 female was fertile. Further, we predicted that it would be easier for the top-ranking male to monopolize females in the small winter enclosure than in the large park. However, the housing conditions had no significant influence on alpha male paternity success. The lack of a relationship between both the number of fertile females and housing condition with paternity success, together with the observation that males did not mate-guard in this

Fig. 3 The alpha male’s ability to monopolize paternity over the course of his tenure. Inward ticks along the x-axis indicate the estimated time of conception and whether the current alpha male sired the forthcoming offspring (top) or not (bottom). Downward facing triangles (gray for alpha male GA and black for his successor MA) and error bars represent mean empirical probabilities (\pm SE) of alpha male paternity over 4 consecutive conceptive periods.



study and in the wild (Cheney *et al.* 1988), suggest that high paternity success is achieved by other means.

The only factor that had a significant effect on paternity success of the alpha male was month into tenure. In the first third of his tenure, the alpha male GA sired all 8 offspring. His success decreased in the second and in the third conceptive period, as he sired only 5 of 9 possible infants, although he clearly remained the dominant male of the group. Competition between the younger males and the alpha male can be expected when benefits of top rank are high (van Noordwijk and van Schaik 2004). The high paternity concentration found in favor of the alpha male in this study suggests that potential for competition was high in this group. Younger males did challenge the older alpha male, and fights between males resulted in injuries. In the first year of the study, the male FR challenged the alpha male. The conflict led to injuries of both males and the challenger was thereafter the lowest ranking and most submissive male toward the top-ranking male for the following years, during which he sired only 1 offspring for which genetic data were available. The youngest male LE, which sired 3 offspring, challenged GA during the last months of his tenure. The relative young age of the lower-ranking males, particularly in the first 6 mo of the study (period I), may have contributed to the high paternity success of GA. However, although the alpha male was observed to mount most often during period I, a large percentage (39%) of copulations were accomplished by lower-ranking males and ≥ 2 of the 3 lower-ranking males were certainly old enough for fertile copulations. Because we observed mounts infrequently and did not record them systematically, one needs to interpret these data with caution. Nevertheless, the finding that the large majority of mounts (88%) took place outside the fertile period, which is in accordance with data from wild vervets (Andelman 1987), would indicate that males have little information about timing of ovulation.

The higher paternity success of the lower-ranking males toward the end of the first alpha male's tenure may represent a shift in female preferences. Sexual conflict over reproduction is ubiquitous in primates, and females usually have difficulties in rejecting male mounting attempts (Muller and Wrangham 2009). However, in vervets, sexual dimorphism is relatively small. The ratio between weights of adult males and the adult females was 1.21 in our study. Probably as a consequence, females in the wild and in captivity have been observed to avoid a large proportion of copulation attempts by males (Andelman 1987; Cheney *et al.* 1988; Keddy 1986), which can be interpreted as a way to exert female choice for preferred mating partners. Unfortunately, we were not able to collect systematically data on female soliciting behavior, but we observed active soliciting and rejections of matings by females, suggesting that female choice also played a role in our study. To maximize genetic and material benefits, e.g., protection for offspring against potentially infanticidal males, females in this study may have favored the dominant male, at least during the first half of his tenure. A shift in female preferences over time also occurred in rhesus macaques (Berard 1999). Here, the longer a male held highest rank, the more females preferred males new to the group, resulting in a decline of copulation frequencies with high-ranking males. Female mate choice in vervets may also explain the large differences in the relationship between number of copulations and rank found over several breeding seasons described in Cheney *et al.* (1988). It is possible that females regarded these males as potential successors of the resident

alpha males and mated preferably with these males to reduce the risk of infanticide after male rank changes (van Schaik and Janson 2000). The slightly higher rates of copulations by lower-ranking males and the relatively high number of rejected copulations in the week of ovulation in Andelman's study could also be interpreted as female choice for preferred mating partners (Fig. 2 in Andelman 1987).

If reproductive success of the alpha male is high, although he does not monopolize females around their fertile periods, paternity may also be decided at the postcopulatory level, e.g., through sperm competition (Birkhead and Møller 1998) or by cryptic female choice (Eberhard 1996; Reeder 2003). Although the importance of these postcopulatory mechanisms remains unclear, they are likely to occur not only in birds but also in primates (Birkhead and Kappeler 2004). Recently, authors examining determinants of reproductive success in Barbary macaques (Brauch *et al.* 2008) and long-tailed macaques (Engelhardt *et al.* 2006) have suggested that postcopulatory mechanisms are important determinants of male reproductive success. Therefore, we can speculate that postcopulatory mechanisms are also responsible for both the high overall alpha male paternity success and the decline with increasing tenure in vervets.

Our results highlight the importance of studying >1 breeding season to understand variation in the relationship between male rank and paternity success within and between species. However, although paternity of almost all offspring could be determined over a relatively long period of 3 yr, we here focused only on 1 group under special conditions and the results may not represent a general pattern in vervets. There are certain limitations of studies carried out in captivity, especially the absence of male transfer and extragroup copulations. Nevertheless, the degree of reproductive synchrony in captivity should affect reproductive success of alpha males in the same way as in the wild, and alpha male tenure length is likely to be related to paternity success in the wild also. Females in the wild may have similar preferences for younger group males, and competition between the males is also likely to increase as the alpha male grows older, especially because vervets are characterized as a species in which dominance takeovers are usually initiated by group males and not by recently immigrated males (Clarke *et al.* 2009). Further studies on free-ranging vervet groups involving endocrinological methods to establish precise timing of ovulation together with genetic paternity testing are needed to increase our understanding of the importance of female choice and postcopulatory mechanisms in this species.

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