



Male and Female Reproductive Success in *Macaca sylvanus* in Gibraltar: No Evidence for Rank Dependence

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*The relationship between social rank and reproductive success is one of the key questions for understanding differences in primate social group structures. We determined the paternity of 18 infants in a social group of Barbary macaques (*Macaca sylvanus*) born over a period of 6 yr in the provisioned, free-ranging colony in Gibraltar. We successfully used 13 pairs of primers of variable microsatellite loci to amplify DNA from blood and hair samples and applied the computer programs CERVUS 2.0 and KINSHIP 1.3 to assign paternity to 13 candidate males. We collected data for 19 females that had given birth to 66 infants over a period of 7 yr. We used paternity analyses and female birth records to test the hypothesis that social rank is correlated with reproductive success. Results showed that numbers of paternities and maternities were equally distributed among all reproducing individuals in the social group regardless of rank. Subadult males reproduced as often as adult males. High-ranking females did not start to reproduce earlier than low-ranking females. Interestingly, there was a tendency toward a positive correlation between the ranks of mothers and the ranks of the corresponding fathers. It might be concluded either that a correlation between social rank and reproductive success is generally absent in Barbary macaques or*

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that artificially favorable environmental conditions in Gibraltar preclude any correlation between social rank and reproductive success.

KEY WORDS: Barbary macaque; microsatellites; paternity analysis; rank correlation; reproductive success.

INTRODUCTION

Whether social rank predicts reproductive success is a matter of active debate in looking at many species of mammals (Dewsbury, 1982; Ellis, 1995). In primate studies, this question is of general interest because many species live in social groups with dominance hierarchies (Walters and Seyfarth, 1987). For females, it is possible to obtain data on reproductive success directly through long-term behavioral observations (Pusey *et al.*, 1997; Rhine *et al.*, 2000; Setchell *et al.*, 2002; van Noordwijk and van Schaik, 1999). For males, by contrast, severe problems are encountered because assignment of paternity is difficult in multimale groups. Although mating success often correlates with social rank (Cowlshaw and Dunbar, 1991), it is not always a reliable indicator of actual reproductive success (Berard *et al.*, 1994; Inoue *et al.*, 1991; Soltis *et al.*, 1997). In recent years, however, the development of polymorphic DNA markers has permitted direct determination of male reproductive success (Bruford and Wayne, 1993; Martin *et al.*, 1992). Surprisingly, it emerged that no clear relationship exists between social rank and reproductive success for some primate species: *Macaca fascicularis* (Shively and Smith, 1985), *M. mulatta* (Berard *et al.*, 1993, 1994), *M. fuscata* (Inoue *et al.*, 1993; Soltis *et al.*, 1997; Takahata *et al.*, 1999), *M. nemestrina* (Gust *et al.*, 1996), and *Pan troglodytes* (Meier *et al.*, 2000). At least 3 reasons could account for this: 1) Socially subordinate individuals may employ alternative strategies to increase their reproductive success (Berard *et al.*, 1994; Constable *et al.*, 2001; Launhardt *et al.*, 2001). 2) Reproductive activities do not necessarily take place only within social groups; extra-group/extra-pair matings can occur (Fietz *et al.*, 2000; Soltis *et al.*, 2001). 3) Captive conditions may weaken or eliminate a relationship that exists under natural conditions. However, various researchers have reported a correlation between social rank and reproductive success in certain primate species, both in the wild and in captivity: *M. mulatta* (Smith, 1993), *M. arctoides* (Bauers and Hearn, 1994), *Macaca fascicularis* (de Ruiter *et al.*, 1994), *Cercocebus torquatus atys* (Gust *et al.*, 1998), *P. paniscus* (Gerloff *et al.*, 1999), *P. troglodytes* (Constable *et al.*, 2001), and *M. fuscata* (Soltis *et al.*, 2001). Hence, inconsistent results are sometimes reported for the same species.

For Barbary macaques (*M. sylvanus*) the relationship between social rank and reproductive success is unclear. Paul *et al.* (1993) found

correlations between male rank and male reproductive success in 3 of 4 mating seasons, but only when subadult males were included in the analysis. In a different study, von Segesser *et al.* (1995) demonstrated that out of 10 adult and subadult males at least 5 and possibly as many as 8 fathered infants. However, in that study no quantitative data on rank relationships were available. For female Barbary macaques, the evidence for a relationship between rank and reproductive success is even less clear (Paul and Küster, 1996). The researchers conducted all of these studies in outdoor enclosures. Barbary macaques form relatively egalitarian societies (Thierry *et al.*, 2000) and are seasonal breeders (Taub, 1980). It might therefore be very difficult for dominant males to monopolize several estrous females simultaneously. Furthermore, female mate choice seems to be important in the species, resulting in promiscuous mating behavior of estrous females (Küster and Paul, 1992). Demographic and ecological factors may also influence the degree of control over mating activities. A correlation should exist between increasing group size and decreasing control, while provisioning of food might eliminate marked differences in body condition and fighting abilities of dominant and subordinate individuals.

A core problem in studies of reproductive success in primates is the time span the data cover. In many cases, only a short period is available for analysis compared with the lifespan of individuals. Yet reproductive success is properly measured as total lifetime fitness. This is important because rank can depend on age (Sprague, 1998), because rank can influence the total length of the reproductive period (Pusey *et al.*, 1997), and/or because the benefits of high rank may be delayed. The problem is especially pronounced in primates, which have very long lifespans. In studies of wild primates, additional problems arise: (1) It is often impossible to obtain samples from all group members for paternity analyses. (2) Extra-group mating cannot be excluded. Appropriate statistical analyses are needed to take such missing data into account.

For our study, we analyzed reproductive success of female and male Barbary macaques living in 1 group in the provisioned, free-ranging colony on Gibraltar over a period of 6 yr for males and 7 yr for females. This period represents approximately one half of the maximum possible reproductive period for males and one third of that for females of the species. We conducted microsatellite analysis to determine paternities and hence male reproductive success using 2 computer-based approaches. We used data on birth records and infant survival to determine female reproductive success and to test whether reproductive success correlates with rank in males and/or females. In line with the potential effects discussed earlier, it is to be expected that any correlation between dominance rank and reproductive success would be expressed more clearly in Gibraltar than in

Salem (Paul *et al.*, 1993). This is because at the former site group size is smaller and clumped food is provided in smaller quantities, allowing better control of mating activities and food allocation by dominant individuals. We also tested whether male reproductive success was related to age and whether the rank of an inferred father correlated with the rank of the infant's mother. Finally, we considered the results in light of ecological aspects and their possible influence on reproductive success.

METHODS

Study Site

We conducted the study in Gibraltar (36°09'N, 5°21'W), having initiated a long-term project in Gibraltar in 1994. After 1995 observers could recognize all individuals older than juveniles individually. During the study period (1995–2001), 200 monkeys on average were living on Gibraltar divided into 6 to 7 social groups. Our research focussed on the Middle Hill group, which ranged in size from 40 to 61 members (Table I). In October 1995, the group consisted of 46 individuals and grew to *ca.* 60 group members in summer 1998 before a splinter group of *ca.* 20 individuals left Middle Hill. During this period, precise information on group size was lacking because the splinter group established its new territory in an inaccessible rocky area, which made it difficult to count newborns and juveniles. Between fall 1998 and summer 2001, the residual group of 40 individuals remaining at Middle Hill grew progressively to reach a total of 61 individuals. During the entire study period, 66 infants were born and the group lost 17 individuals. Among the latter, 4 individuals are known to have died (2 adult females and 2 infants), 3 juvenile males emigrated to another group, and 7 identified individuals and 3 unidentified juvenile individuals disappeared for unknown reasons. We did not observe any male immigrants. Most (6 of 7) of the identified group members that disappeared were adult males. It is unknown whether

Table I. Age and sex composition of the Middle Hill group in Gibraltar, before and after the group fission in summer 1998, following the categories of Merz (1984)

	Adult males	Adult females	Subadult males	Subadult males	Juveniles	Infants	Sum
Pre-fission period 1995–1998	11–12	8–10	2–4	2–5	14–20	7–9	46–60 ^a
Post-fission period 1998–2001	4–7	8–13	4–6	3–6	14–19	7–12	40–61

^aEstimation of group size during the fission process (see text for details).

they died or whether the Gibraltar population management authority removed them. Male migration rate seems to be very low in Gibraltar and typically occurs at a relatively young age (unpublished data of the Zürich research team). Three emigrating males left the group when they were 3, 4, and 5 yr old, respectively. As we could not identify all 3-yr-old individuals individually, this observed number of migrations must be considered as a minimum. The different social groups in Gibraltar seem to be very distinct and intergroup encounters were rarely observed (Semple, personal communication; personal observation). We did not observe any copulations between out-group males and the females from Middle Hill during more than 1000 h of observation on mating behaviour between October 1996 and February 1997 (Semple, personal communication).

The home range of the Middle Hill group is situated in a military area without public access. Although well habituated to humans, these individuals had little contact with tourists, unlike the other social groups (O'Leary and Fa, 1993). To prevent the macaques from ranging down into town, they were fed with fruits and vegetables once a day by the Gibraltar population management authority. As the provisioned food did not satisfy their daily needs, however, the individuals spent considerable time feeding on natural resources such as seeds, roots, fruits, and flowers.

Behavioral Data

To evaluate the social hierarchy, we determined pairwise rank relationships. Between 1996 and 2001, 5 researchers contributed to the data set during the following 4 study periods: October 1996 to February 1997 (Möhr, 1999; Semple, 1998), May to July 1997 (Chervet, 1998), July-October 1999 (Kümmerli, 2000), and April to July 2000 (Roberts, 2004). All observers used only dyadic clear dominance interactions, including both aggressive and submissive behavior (Semple, 1998). We scored a total of 3324 agonistic interactions (985 interactions between 2 males and 2339 interactions between 2 females). We recorded numbers of infants and mother-infant pairs every year during or shortly after the birth season.

Fission of the Middle Hill group occurred in summer 1998, before which time the male hierarchy remained stable. For assessment of male reproductive success, we considered all infants for which we recorded births between 1995 and 1998. We also included 6 infants born in the years 1993 and 1994 because their age and sex could be determined easily at the beginning of our data collection in 1995. We have no information about group size and group composition for these 2 yr. For this period, we assumed that no male migration occurred and that the hierarchy was the same as

for the subsequent years (1995–1998). These assumptions seem to be justified because male migration rate was very low and the hierarchy remained stable during subsequent years. However, the male dominance hierarchy changed dramatically after fission of the group. The keepers culled the 3 top-ranking males after they became members of the splinter group (see later). In the residual Middle Hill group, the fifth-ranking male overtook the fourth-ranking male to become the new top-ranking male. Because of these rank changes, infants sired after the group fission could not be considered for paternity analyses. To assess female reproductive success, we used the 1995–2001 birth records. Even after troop fission, no female moved up the hierarchy relative to other females, although the absolute rank of course changed because of the smaller total number of females in each group. For initial analysis, we took the average linear hierarchy over all years, and placed young females that started to reproduce during the period covered in the rank class of their matriline (Paul and Küster, 1987). However, we also separated the data set into pre- and post-fission subsets and analyzed these subsets separately.

Blood and Hair Sampling

In September 1999, we either trapped 32 individuals remaining in the Middle Hill group in a large cage or sedated them directly via a blowpipe (Telinject). We obtained EDTA-buffered blood samples by venipuncture from the femoral vein. We used Ketaminol 100 mg/ml (0.2 ml/kg body weight) as the anesthetic. Previously, in summer 1998, the Middle Hill troop had split into 2 subunits. One subunit moved down to a hotel, where it caused considerable damage, and consequently the keepers culled the macaques. At this time, we collected 22 additional samples from individuals in that subunit by plucking hairs. The total sample set ($n = 54$) represented almost the entire original Middle Hill group and included 13 potential fathers, 16 known mother-infant pairs, and 16 infants with unknown mothers. We were unable to obtain samples from 5 potential fathers because the males disappeared from the troop before samples could be collected. For the analysis, we pooled the 5 males and allocated an average rank.

DNA Extraction and Microsatellite Analysis

We centrifuged blood samples and extracted nuclear DNA from the separated leucocytes using the Genomix Whole Blood Extraction kit (Labortechnik Fröble GmbH, Germany). We treated hair roots with Chelex 5% following Morin (1992).

We successfully used 13 pairs of oligonucleotide primers to amplify microsatellites: 1 primer (*MFGT17*) designed for Japanese macaques (Inoue and Takenaka, 1993) and 12 systems were human primers. It is known that 9 of the latter systems—*DIS207*, *D2S141*, *D6S311*, *D7S503*, *D8S1106*, *D11S925*, *D16S420*, *D17S791*, and *D18S536*—show variation in Barbary macaques (Lathuillière *et al.*, 2001; von Segesser, 1999; von Segesser *et al.*, 1999) and that the 3 remaining systems—*D2S305*, *D3S1279*, and *D4S243*—show polymorphism in other Old World monkeys (Nair *et al.*, 2000; von Segesser, personal communication) and were successfully amplified in *M. sylvanus*. Most of the microsatellite sequences we examined consisted of CA repeats, but the 3 markers *D4S243*, *D8S1106*, and *D18S536* contained GATA tetranucleotide repeats.

We amplified the template DNA in a 25- μ l reaction volume containing 0.06 M Tris, 0.015 M $(\text{NH}_4)_2\text{SO}_4$, 1.5 mM MgCl_2 , 0.78 M dimethyl sulfoxide (DMSO), 400 μ M of each dNTP, 0.3 μ M of each primer, and 1.25 U of *Taq* polymerase. For the *MFGT17* polymerase chain reaction (PCR) mix, we added 1 μ l of 0.1 M MgCl_2 . Amplification took place in a 9700 Thermal Cycler (Applied Biosystems) using 2 different PCR procedures. We used the first procedure, described by von Segesser (1999), for the 9 allele systems *MFGT17*, *DIS207*, *D2S141*, *D2S305*, *D3S1279*, *D6S311*, *D7S503*, *D11S925*, and *D17S791*. For the 4 systems *D4S243*, *D8S1106*, *D16S420*, and *D18S536* we used the second PCR procedure, based on a touch-down PCR program with the following conditions: 1) denaturing phase: 5 min at 94°C, 2) touch-down phase: 4 \times 3 cycles with annealing temperature decreasing in 2°C-steps with 94°C/ T_{1-4} /72°C, 45 s/60 s/90 s, 3) optimal annealing temperature phase: 25 cycles under the same conditions with annealing temperature T_5 . Annealing temperatures T_1 – T_5 varied between markers.

Following PCR amplification, we electrophoresed 2 μ l of the reaction mixture through a Spreadex gel for 2–5 h on the submerged gel electrophoresis system supplied by Elchrom Scientific (Apparatus SEA 2000) (Hourihan *et al.*, 2000). We stained the gels for 45 min in SYBR-Gold (Molecular Probes) and destained them in DST-destaining solution (Elchrom Scientific) for 30 min. We standardized allele size between gels by running the M3 Marker (Elchrom Scientific).

Statistical Analyses

We determined paternity on the basis of 2 maximum likelihood methods via the computer programs KINSHIP 1.3.1 (Goodnight and Queller, 1999) and CERVUS 2.0 (Marshall *et al.*, 1998). KINSHIP 1.3.1 conducts pairwise comparison between every infant-mother pair and every potential father, testing the primary hypothesis that a male fits the pedigree

relationship of a father ($h_1: R_p = 1, R_m = 0$) against the null hypothesis that a male is unrelated to the infant ($h_0: R_p = 0, R_m = 0$). One compares the calculated likelihood ratio ($\log h_1/h_0$) with the critical value evaluated from a simulation and provided with a confidence level. CERVUS 2.0 conducts a comparison between an infant-mother pair and all the potential fathers in the data set. A LOD score (i.e., the logarithm of the likelihood ratio) is calculated for every potential father and then listed. The difference between the LOD scores of the male with the highest value and the male with second highest value is the Δ -criterion (Δ LOD) (Marshall *et al.*, 1998). Δ LOD is compared with the critical Δ values calculated after a simulation and provided with a statistical confidence level. The simulation was based on allele frequency data from the entire study group. Parameters used for the simulation differed from year to year and we based our choices on the following criteria: 1) total number of candidate males = 12–15; 2) proportion of candidate males sampled = 0.58–0.87; 3) proportion of data typed = 0.87–0.91; and 4) rate of typing errors = 0.01 (default option of the program CERVUS). We chose the confidence levels as proposed by Marshall *et al.* (1998) (relaxed confidence $\geq 80\%$, strict confidence $\geq 95\%$). We performed Spearman rank correlation tests to examine relationships between rank and reproductive success in males and females. To test whether reproductive success differs between adult and subadult males and whether the onset of birth in females is rank dependent, we applied Fisher's exact probability test.

RESULTS

Diversity of Microsatellite Markers

We detected a total of 40 alleles in the 13 microsatellite systems, giving an average of 3.1 alleles per locus with a range from 2 to 5 alleles per locus (Table II). Observed heterozygosity ranged between 0.08 and 0.90. Only one locus (*DI6S420*) showed a significant deviation from Hardy-Weinberg equilibrium. In this case, observed heterozygosity was higher (0.90) than expected heterozygosity (0.76). The presence of one or more null alleles can be excluded as a possible explanation for the observed deviation from Hardy-Weinberg equilibrium because observed heterozygosity should be significantly lower than expected heterozygosity. To test whether the use of this locus affects our results, we conducted 2 separate analyses, one including *DI6S420* and one excluding it. When we excluded *DI6S420*, all the unresolved paternities remained unresolved, 13 paternity assignments did not differ, in 4 cases paternity assignment remained the same but lost some statistical power, and in only 1 case did

Table II. The 13 microsatellite loci used for paternity analysis

Locus	No. of animals typed	No. of alleles in Gibraltar	H _O	H _E	HWE <i>p</i> -value
<i>MFGT17</i>	25	3	0.64	0.62	0.72
<i>D1S207</i>	54	2	0.25	0.22	1.00
<i>D7S503</i>	41	3	0.68	0.54	0.27
<i>D11S925</i>	41	3	0.54	0.52	1.00
<i>D17S791</i>	41	2	0.44	0.47	0.74
<i>D8S1106</i>	53	3	0.32	0.28	0.77
<i>D16S420</i>	42	5	0.90	0.76	<0.0001
<i>D18S536</i>	46	2	0.46	0.47	1.00
<i>D2S141</i>	48	2	0.08	0.08	1.00
<i>D6S311</i>	46	5	0.59	0.68	0.14
<i>D4S243</i>	30	5	0.73	0.73	0.90
<i>D2S305</i>	47	2	0.28	0.27	1.00
<i>D3S1279</i>	42	3	0.69	0.55	0.19

Note. H_O: Observed heterozygosity; H_E: expected heterozygosity; HWE: Hardy-Weinberg-equilibrium.

paternity assignment change. In the last case, the only remaining potential father could be excluded from paternity only with the information of locus *D16S420*, and paternity was then assigned to the pool of the 5 untyped males. These results showed that the use of *D16S420* did not alter paternity assignment, but increased statistical power. Hence, as genetic variability was in general quite low at the microsatellite loci genotyped, the locus *D16S420* was included in the analyses and these results are presented here.

Paternity Analysis

All results for the paternity analysis are in Table III. It proved possible to determine 13 (81.3%) paternities for the 16 known mother-infant pairs. KINSHIP and CERVUS yielded closely congruent results. Both analyses assigned paternity to the same male in 9 cases (3 were confirmed at the 95% confidence level and 6 at the 80% confidence level for the CERVUS analysis. Significance levels assigned by KINSHIP ranged between $p = 0.05$ and $p = 0.001$). In 4 cases, we excluded all sampled males from paternity and assigned paternity to the pool of the 5 untyped males. In 2 cases, CERVUS could not resolve the paternity because in both cases 2 males had a high LOD score, and KINSHIP showed that both of these males significantly possess the genetic constitution of fathers. It is therefore unlikely that any of the untyped males fathered the infants, and we assigned paternity with a value of 0.5 to both males (split paternity). We were able to determine 3 (18.8%) paternities of the 16 infants for which neither parent

Table III. Paternity analysis

	Paternity assigned by CERVUS and confirmed by KINSHIP		Split paternity assigned by KINSHIP	Paternity assigned to untyped males	Unresolved
	≥95% (strict)	≥80% (relaxed)			
Infants with known mothers (<i>n</i> = 16)	3	6	2	4	1
Infants with unknown mothers (<i>n</i> = 16)	0	2	0	1	13
Total	3	8	2	5	14

Note. Confidence levels for CERVUS were set at ≥95% (strict level) and at ≥80% (relaxed level). KINSHIP significance level varied between $p = 0.001$ and $p = 0.05$.

was known. In 2 cases, we assigned paternity to the same male by both programs and confirmed this at the 80% confidence level (CERVUS) and with a p -value between $p = 0.05$ and $p = 0.01$ (KINSHIP). In one case, we excluded all males and assigned paternity to the pool of 5 untyped males. This low determination rate can be explained by the facts that we did not know the identity of the mother and that for these infants we had predominantly hair samples, which did not yield good results in our microsatellite analysis.

For subsequent analysis, we considered only males that had at least 3 reproductive years during the study period ($n = 10$, mean reproductive years = 5.4). There is no significant correlation between the rank of a male and the number of infants sired per reproductive year (Fig. 1; Spearman: $r_s = -0.20$, $n = 10$, $p = 0.58$). This result did not change after excluding subadult males (Spearman: $r_s = -0.01$, $n = 10$, $p = 0.98$). We inferred the fathers of 7 male and 11 female offspring. Male rank did not correlate either with the number of male infants sired (Spearman: $r_s = -0.02$, $n = 10$, $p = 0.95$) or with the number of female infants fathered (Spearman: $r_s = -0.06$, $n = 8$, $p = 0.85$).

Adult males sired 15 infants and subadult males fathered 3 infants. The 3 subadult males were 4.5 yr, 5.5 yr, and 6.5 yr of age, respectively, when they sired their offspring. Between 1993 and 1998, the group included on average 10.5 adult males and 3.2 subadult males. Hence, adult males did not sire more infants than expected by chance, and hence we could not detect any difference between these 2 categories (Fisher's exact test: $p = 0.5$). We found some indication for a relationship between male age and reproductive success. In our study group, males that were between

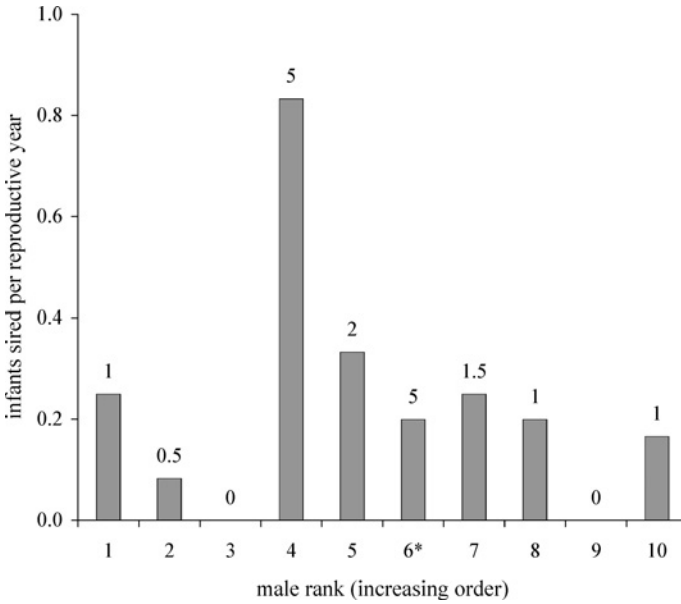


Fig. 1. Male reproductive success between 1993 and 1998 measured as infants sired per year. Numbers above the columns indicate the total numbers of infants sired. 6* represents the pooled group for the five untyped males.

4 and 8 yr of age reproduced at a low rate. Reproductive success increased and peaked between the ages of 9 and 10 yr and slowly decreased with increasing age thereafter (Fig. 2).

In summary, 2 of the group males sired no infant, 5 fathered 1 offspring (corresponding to 0.5–1.5 assigned paternities due to split paternities), 1 sired 2 infants, and 1 male fathered 5 infants. Although we do not know the distribution of the 5 paternities among the 5 untyped males, it seems that paternities are equally distributed among all males (adults and subadults), with the exception of the male with the fourth rank from the bottom, which had above-average reproductive success (Fig. 1). This surprising degree of reproductive success in a comparatively low-ranking male has no obvious explanation. His low rank is not an artifact resulting from the missing males, as at least 5 remaining males ranked above him.

Maternity Analysis

Between 1995 and 2001, at least 66 infants were born in 75 female reproductive years (88%) to 19 different females. We do not know the exact

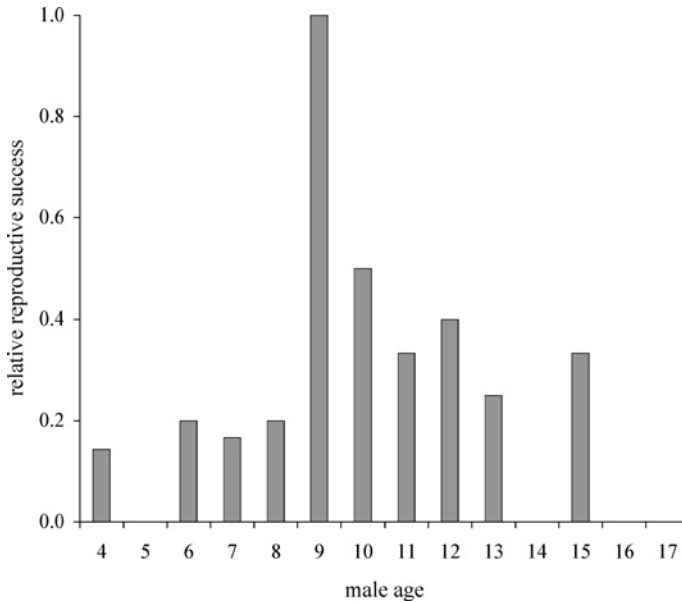


Fig. 2. Relative reproductive success in relation to male age (in years). Relative reproductive success is measured as the number of infants sired by males of a certain age class divided by the number of males in this age class ($N = 18$ males-infant pairs). The pooled group of the five untyped males was allocated the average age.

number of infants born because observers were not always present during the birth season. Some infants might have died shortly after birth. However, infant mortality seemed to be generally very low in Gibraltar. We observed only 2 infant deaths within the first 3 months of life and a maximum of 4 juveniles (3–4 yr old) disappeared from the group. Whether they died or moved to another group is unknown.

For subsequent analysis, we considered only females that had at least 3 reproductive years during the study period ($n = 12$, mean reproductive years = 5.4). Between them the 12 females had a total of 64 reproductive years. During this time, 57 infants were born (89% of possible reproduction) and 55 infants survived (86% of possible reproduction). Nine females out of 12 had an infant every year and 7 females had a surviving offspring every year (Fig. 3). These results clearly show that there was almost no variance in reproductive output between females. It was therefore impossible to find any association between the rank of a female and her reproductive success over the whole study period (or for the pre- and the post-fission periods taken separately). In total, 35 male infants and 31 female infants

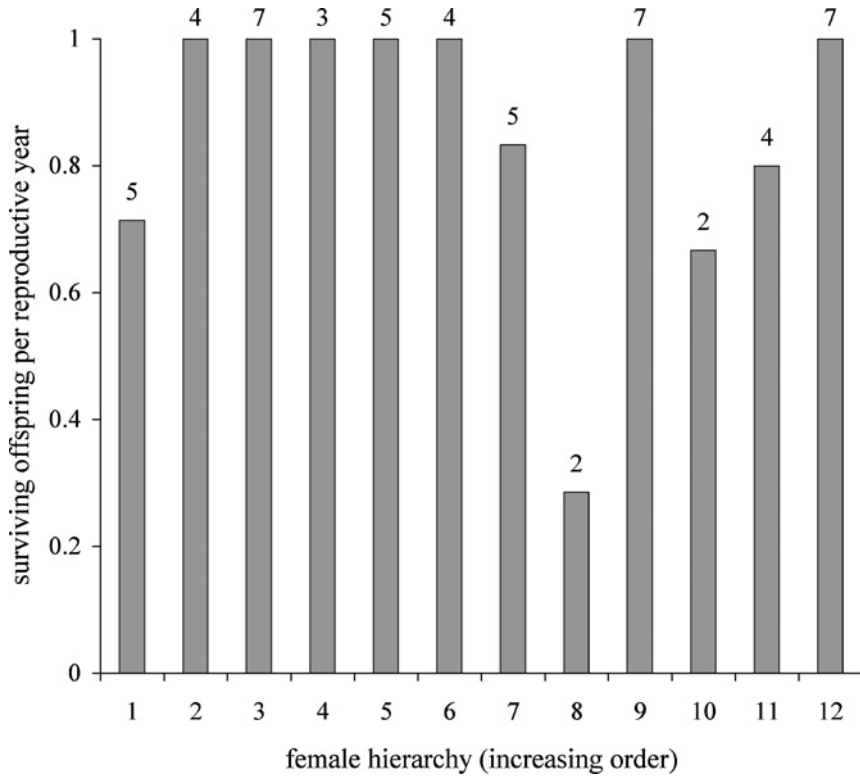


Fig. 3. Female reproductive success between 1995 and 2001 measured as surviving infants per reproductive year. Numbers above the columns indicate the total numbers of infants surviving for the first 3 months of life.

were born. Female rank does not correlate either with the number of male infants produced (Spearman: $r_s = 0.14, n = 12, p = 0.66$) or with the number of female infants produced (Spearman: $r_s = -0.07, n = 12, p = 0.82$).

Female Barbary macaques can conceive for the first time at the age of 3.5 yr and give birth at the age of 4 yr (Merz, 1984). In this study, 4 females conceived at 3.5 yr and 10 conceived later. High-ranking females did not conceive earlier than low-ranking females (Fisher's exact test: $p = 0.17$). In fact, females that conceived at 3.5 yr either lost the infant (2 cases) or did not give birth in the following year (2 cases). As a general rule, then, females in the Middle Hill group have their first infant at the age of 5 and produce 1 infant every year thereafter. This is clearly borne out by the average interbirth interval (IBI) of 1.14 yr. As Barbary macaques are strictly seasonal breeders, the minimum possible IBI is 1 yr.

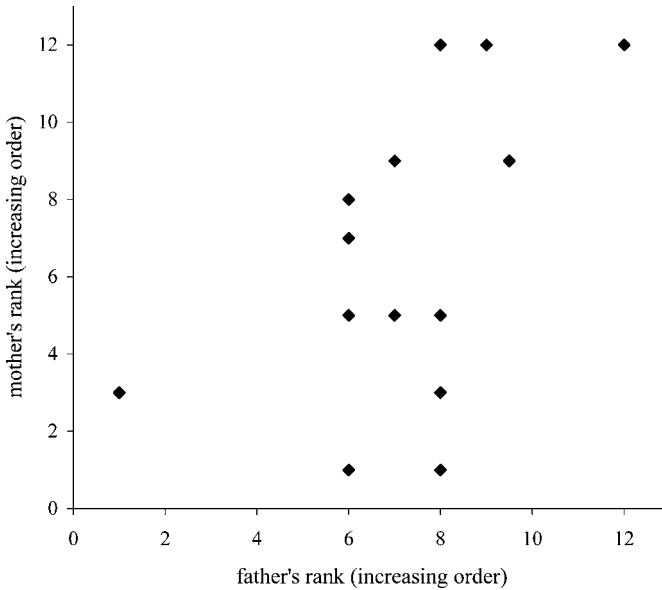


Fig. 4. Ranks of mothers in relation to ranks of the corresponding fathers. There is a tendency for a positive correlation between rank-pairs ($p = 0.061$).

Relationship Between the Rank of the Mother and the Rank of the Father

We knew the identity of the mother and the father for 15 infants analyzed in this data set. We allocated social ranks to each mother-father pair (Fig. 4). For split paternities, we allocated the mean of the 2 male's ranks. A not quite significant positive correlation resulted (Spearman: $r_s = 0.43$, $n = 15$, $p = 0.061$).

DISCUSSION

It was possible to analyze the reproductive success of 12 females that gave birth to 57 infants and of 9 males that sired 18 offspring. The lack of any correlation between social rank and reproductive success for both males and females is a striking outcome of this long-term study. For females, support for this conclusion is strong because the birth record is almost complete. For males, only 41.9% of all surviving infants could be analysed with respect to paternity, but results suggest that reproductive success is evenly distributed among males (adults and subadults). This outcome

could potentially change if it were possible to include all infants sired during the study period. But this seems unlikely because there is no obvious source of bias in our sample of infants. With the analysis conducted with CERVUS, the effect of missing potential fathers can be simulated. The more data for potential fathers are lacking, the more difficult it is to attribute paternities to the remaining males, and high confidence levels are hard to attain. This explains why we could confirm many of our paternities only at the 80% level, although significance levels from the KINSHIP program ranged from $p = 0.001$ to $p = 0.05$. It is important to include such simulations in paternity analysis, especially for wild-living primates with which there will always be missing potential fathers or outgroup males. The CERVUS analysis has further advantages: Typing rate of markers must be included, typing errors are estimated, and paternity analysis can be conducted without knowing the mother. Although these factors lead to a decrease in confidence level, we regard our results as reliable because they simulate the true situation.

Our results indicate that male reproductive success is related to age. In our study group, males were most successful between 9 and 10 yr of age, while reproductive success was low before this period and declined thereafter. If this observation is generally valid for this species, then the time window for successful reproduction is very narrow. This might increase the competition between males. The observed pattern differs somewhat from that observed by Paul *et al.* (1993), who reported that old males also reproduced successfully. However, the conclusion from the present study must be treated with caution because of the small sample size.

Although we detected no correlation between social rank and reproductive success for females or males, there is a trend toward one relationship between these 2 factors: High-ranking males tended to sire infants of high-ranking mothers, while low-ranking males tended to father infants of low-ranking mothers. The correlation was just below the threshold of significance ($p = 0.061$). We would not anticipate a strong correlation because Barbary macaques, especially females, show very promiscuous mating behaviour (Küster and Paul, 1992), such that paternity certainty is expected to be very low. Another study on the same social group showed that social affiliation between high-ranking males and females is very common (Kümmerli and Martin, in preparation). Coalition formation and infant carrying correlated with one another and involved mainly members of high-rank classes. The correlation between the mother's and the father's rank might also indicate that the benefit of having a high rank might be masked in this semicaptive social group owing to artificially favorable environmental conditions. We did, in fact, find evidence that social rank influences a

female's body condition: we found a significant positive correlation between the rank of an adult female and her body mass (R. K. unpublished data), which raises the possibility that high-ranking females might have higher reproductive success under the harsher environmental conditions prevailing in the wild in Morocco and Algeria. Moreover, because high-ranking males tend to father infants of high-ranking females, this would lead to higher reproductive success for high-ranking males as well.

Our study provides further support for the conclusion that the relationship between social rank and reproductive success is heterogeneous between and within species in *Macaca*. At first sight, this is surprising because the social system is—superficially, at least—very similar in all macaque species, which live in large multimale-multifemale groups with linear rank orders for both sexes and with females as the philopatric sex and daughters inheriting the rank of their mothers. But there are also notable differences, mainly in the seasonality of breeding behavior, the level of aggressiveness, and the rigidity of the hierarchy (Fa and Lind, 1996; Matsumura, 1999; Thierry, 2000). Breeding seasonality is one important factor that seems to explain some of the variation between species in the relationship between dominance rank and reproductive success (Paul, 1997). The expectation from hypothetical considerations is that in nonseasonal breeders male rank position should be more tightly linked to reproductive success than in seasonal breeders because few females are in estrus at any one time and dominant males can therefore more easily exert control over mating activities. Indeed, some authors found a positive correlation in some nonseasonal breeders: *M. fascicularis* (de Ruiter *et al.*, 1994), *M. arctoides* (Bauers and Hearn, 1994), and *M. sinica* (Keane *et al.*, 1997). By contrast, researchers did not detect a clear relationship between male rank and reproductive success in some seasonal breeders: *M. fuscata* (Takahata *et al.*, 1999), *M. mulatta* (Berard *et al.*, 1993), and *M. sylvanus* (Paul *et al.*, 1993; von Segesser *et al.*, 1995; and this study). However, for some of them results from different studies were inconsistent: *M. mulatta* (Berard *et al.*, 1993; Smith, 1993), *M. fuscata* (Soltis *et al.*, 1997, 2001) and *M. fascicularis* (de Ruiter *et al.*, 1994; Shively and Smith, 1985). Intraspecific variation in the relationship between social rank and reproductive success might reflect differences in group size (and sex ratio) or differences in resource abundance (ecological factors), or both. Food provisioning of free-ranging groups not only eliminates marked differences in body condition between dominant and subordinate individuals but also tends to lead to larger groups (Paul and Küster, 1988). Both factors might decrease the ability of a dominant individual to control mating activities, thus reducing any potential correlation between dominance rank and reproductive success. This could explain why some authors found positive correlations with wild

groups of *M. fascicularis* and *M. fuscata* (de Ruiter *et al.*, 1994; Soltis *et al.*, 2001) whereas this was not the case with provisioned free-ranging groups of the same species (Shively and Smith, 1985; Soltis *et al.*, 1997). However, studies on rhesus macaques have shown that the relationship between male dominance rank and reproductive success may differ even between different free-ranging social groups (Berard *et al.*, 1993; Bercovitch and Nurnberg, 1996; Smith, 1993). Indeed, Berard (1999) showed that the effect of rank on reproductive activity varied from year to year according to group composition, such that the relationship between social rank and reproductive success might be expressed in some breeding periods but not in others.

For the Barbary macaque, it can be predicted that the relationship between dominance rank and reproductive success should be expressed more clearly in the Gibraltar population than in the Salem population because the Gibraltar macaques live in a more natural environment, permitting unconstrained group sizes and devotion of much time to feeding on natural resources. However, this did not prove to be the case, perhaps because the Gibraltar population also benefits from relatively favorable conditions, as well. There are no natural predators, there is no limitation of food or water, and there are no harsh winters as in their natural habitats in Algeria and Morocco (Fa, 1986). These factors may explain why in Gibraltar all females generally gave birth to an infant every year, such that no difference in reproductive success depending on rank could be found. For males, the lack of any connection between rank and reproductive success might be due to strict breeding seasonality and/or the promiscuous mating behavior of females. Furthermore, there is a difference between the findings from the study conducted in Salem and ours, in that in Gibraltar subadult males were as successful as adult males in breeding. Perhaps there are alternative mating strategies for low-ranking and subadult males. The habitat in Gibraltar is very rocky, with many niches, caves, and shrubs, and group members can disperse over a wide area (personal observations). This might increase the likelihood of males being able to pursue alternative strategies more successfully than in Salem.

In summary, we demonstrated that there is no correlation between social rank and reproductive success for either male or female Barbary macaques in Gibraltar. This may be attributable to breeding seasonality and/or alternative strategies in males and artificially favorable environmental conditions for females, but these potential explanations remain hypothetical. The tendency for a positive correlation between the ranks of mothers and fathers may indicate that the benefits of having a high rank are masked in this provisioned social group. Reproductive success was related to male age, such that 9- and 10-yr-old males were the

most successful. Further studies are needed in which social groups of different sizes living under different environmental conditions can be compared, and male mating behavior should ideally be investigated under natural conditions. Moreover, comparison of the social systems of different macaque species may help to determine the reasons for different findings concerning the relationship between social rank and reproductive success.

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REFERENCES

- Bauers, K. A., and Hearn, J. P. (1994). Patterns of paternity in relation to male social rank in the stump-tailed macaque, *Macaca arctoides*. *Behaviour* 129: 149–176.
- Berard, J. D. (1999). A four-year study of association between male dominance rank, residency status and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates* 40: 159–175.
- Berard, J. D., Nurnberg, P., Epplen, J. T., and Schmidtke, J. (1993). Male rank, reproductive behavior, and reproductive success in free-ranging rhesus macaques. *Primates* 34: 481–489.
- Berard, J. D., Nurnberg, P., Epplen, J. T., and Schmidtke, J. (1994). Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour* 129: 177–201.
- Bercovitch, F. B., and Nurnberg, P. (1996). Socioendocrine and morphological correlates of paternity in rhesus macaques (*Macaca mulatta*). *J. Reprod. Fert.* 107: 59–68.
- Bruford, M. W., and Wayne, R. K. (1993). Microsatellites and their application to population genetic studies. *Curr. Opin. Genet. Dev.* 3: 939–943.
- Chervet, V. (1998). *Auswirkungen der Geburt auf das Sozialverhalten bei Berberaffen (Macaca sylvanus, L.) auf Gibraltar*, MSc thesis, University of Zurich, Zurich.
- Constable, J. L., Ashley, M. V., Goodall, J., and Pusey, A. E. (2001). Noninvasive paternity assignment in Gombe chimpanzees. *Mol. Ecol.* 10: 1279–1300.
- Coote, T., and Bruford, M. W. (1996). Human microsatellites applicable to the analysis of genetic variation in apes and Old World monkeys. *J. Hered.* 87, 406–410.

- Cowlshaw, G., and Dunbar, R. I. M. (1991). Dominance rank and mating success in male primates. *Anim. Behav.* 41: 1045–1056.
- de Ruiter, J. R., van Hooff, J. A. R. A. M., and Scheffrahn, W. (1994). Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour* 129: 203–224.
- Dewsbury, D. A. (1982). Dominance rank, copulatory behavior, and differential reproduction. *Q. Rev. Biol.* 57: 135–159.
- Ellis, L. (1995). Dominance and reproductive success among nonhuman animals—a cross-species comparison. *Ethol. Sociobiol.* 16: 257–333.
- Fa, J. E. (ed.) (1986). *Use of Time and Resources by Provisioned Troops of Monkeys*, Karger, Basel, Switzerland.
- Fa, J. E., and Lind, R. (1996). *Evolution and Ecology of Macaque Societies*, Cambridge University Press, New York.
- Fietz, J., Zischler, H., Schwiegk, C., Tomiuk, J., Dausmann, K. H., and Ganzhorn, J. U. (2000). High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behav. Ecol. Sociobiol.* 49: 8–17.
- Gerloff, U., Hartung, B., Fruth, B., Hohmann, G., and Tautz, D. (1999). Intra-community relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proc. R. Soc. Lond. B.* 266: 1189–1195.
- Goodnight, K. F., and Queller, D. C. (1999). Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* 8: 1231–1234.
- Gust, D. A., Gordon, T. P., Gergits, W. F., Casna, N. J., Gould, K. G., and McClure, H. M. (1996). Male dominance rank and offspring-initiated affiliative behaviors were not predictors of paternity in a captive group of pigtail macaques (*Macaca nemestrina*). *Primates* 37: 271–278.
- Gust, D. A., McCaster, T., Gordon, T. P., Gergits, W. F., Casna, N. J., and McClure, H. M. (1998). Paternity in sooty mangabeys. *Int. J. Primatol.* 19: 83–94.
- Houriha, R. N., O'Sullivan, G. C., and Morgan, J. G. (2000). High-resolution detection of loss of heterozygosity of dinucleotide microsatellite markers. *BioTechniques* 30: 342–346.
- Inoue, M., Mitsunaga, F., Nozaki, M., Ohsawa, H., Takenaka, A., Sugiyama, Y., Shimizu, K., and Takenaka, O. (1993). Male dominance rank and reproductive success in an enclosed group of Japanese macaques: with special reference to post-conception mating. *Primates* 34: 503–511.
- Inoue, M., Mitsunaga, F., Ohsawa, H., Takenaka, A., Sugiyama, Y., Gaspard, S. A., and Takenaka, O. (1991). Male mating behaviour and paternity discrimination by DNA fingerprinting in a Japanese macaque group. *Folia Primatol.* 56: 202–210.
- Inoue, M., and Takenaka, O. (1993). Japanese macaque microsatellite PCR primers for paternity testing. *Primates* 34: 37–45.
- Keane, B., Dittus, W. P. J., and Melnick, D. J. (1997). Paternity assessment in wild groups of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka using molecular markers. *Mol. Ecol.* 6: 267–282.
- Kümmerli, R. (2000). *Das soziale Umfeld der Babies der Berberaffen (Macaca sylvanus) in Gibraltar*, MSc thesis, University of Zurich, Zurich.
- Küster, J., and Paul, A. (1992). Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). *Behaviour* 120: 192–217.
- Lathuillière, M., Ménard, N., and Crouau-Roy, B. (2001). Sequence conservation of nine Barbary macaque (*Macaca sylvanus*) microsatellite loci: implication of specific primers for genotyping. *Folia Primatol.* 72: 85–88.
- Launhardt, K., Borries, C., Hardt, C., Epplen, J. T., and Winkler, P. (2001). Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. *Anim. Behav.* 61: 53–64.
- Marshall, T. C., Slate, J., Kruuk, L. E. B., and Pemberton, J. M. (1998). Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* 7: 639–655.

- Martin, R. D., Dixon, A. F., and Wickings, E. J. (1992). *Paternity in Primates: Genetic Tests and Theories*, Karger, Basel, Switzerland.
- Matsumura, S. (1999). The evolution of “egalitarian” and “despotic” social systems among macaques. *Primates* 40: 23–31.
- Meier, C., Hemelrijk, C. K., and Martin, R. D. (2000). Paternity determination, genetic characterization, and social correlates in a captive group of chimpanzees (*Pan troglodytes*). *Primates* 41: 175–183.
- Merz, E. (1984). Definition of age-sex classes for the Barbary macaque. In Fa, J. E. (ed.), *The Barbary Macaque: A Case Study in Conservation*, Plenum Press, New York, pp. 335–346.
- Möhr, F. (1999). *Soziale Aspekte während der Paarungssaison bei weiblichen und männlichen Berberaffen (Macaca sylvanus) in Gibraltar*, MSc thesis, University of Zurich, Zurich.
- Morin, P. A., and Woodruff, D. S. (1992). Paternity exclusion using multiple hypervariable microsatellite loci amplified from nuclear DNA of hair cells. In Martin, R. D., Dixon, A. F., and Wickings, E. J. (eds.), *Paternity in Primates: Genetic Tests and Theories*, Karger, Basel, pp. 63–81.
- Nair, S., Ha, J., and Rogers, J. (2000). Nineteen new microsatellite DNA polymorphisms in pigtailed macaques (*Macaca nemestrina*). *Primates* 41: 343–350.
- O’Leary, H., and Fa, J. E. (1993). Effects of tourists on Barbary macaques at Gibraltar. *Folia Primatol.* 61: 77–91.
- Paul, A. (1997). Breeding seasonality affects the association between dominance and reproductive success in non-human male primates. *Folia Primatol.* 68: 344–349.
- Paul, A., and Küster, J. (1987). Dominance, kinship and reproductive value in female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Behav. Ecol. Sociobiol.* 21: 323–331.
- Paul, A., and Küster, J. (1988). Life history patterns of semifree-ranging Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. In Fa, J. E., and Southwick, C. H. (eds.), *Ecology and Behavior of Food-Enhanced Primate Groups*, Alan R. Liss, New York, pp. 199–228.
- Paul, A., and Küster, J. (1996). Differential reproduction in male and female Barbary macaques. In Fa, J. E., and Lindburg, D. G. (eds.), *Evolution and Ecology of Macaque Societies*, Cambridge University Press, Cambridge, UK, pp. 293–317.
- Paul, A., Küster, J., Timme, A., and Arnemann, J. (1993). The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). *Primates* 34: 491–502.
- Pusey, A., Williams, J., and Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277: 828–831.
- Rhine, R. J., Norton, G. W., and Wasser, S. K. (2000). Lifetime reproductive success, longevity, and reproductive life history of female yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Am. J. Primatol.* 51: 229–241.
- Roberts, S. G. B. (2004). *Hiding Behaviour and Social Sensitivity in Non-Human Primates*, PhD thesis, University of Sussex, Brighton.
- Semple, S. (1998). The function of Barbary macaque copulation calls. *Proc. R. Soc. Lond. B.* 265: 287–291.
- Setchell, J. M., Lee, P. C., Wickings, E. J., and Dixon, A. F. (2002). Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *Int. J. Primatol.* 23: 51–68.
- Shively, C., and Smith, D. G. (1985). Social-status and reproductive success of male *Macaca fascicularis*. *Am. J. Primatol.* 9: 129–135.
- Smith, D. G. (1993). A 15-year study of the association between dominance rank and reproductive success of male rhesus macaques. *Primates* 34: 471–480.
- Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X., and Takenaka, O. (1997). Sexual selection in Japanese macaques II: female mate choice and male-male competition. *Anim. Behav.* 54: 737–746.

- Soltis, J., Thomsen, R., and Takenaka, O. (2001). The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Anim. Behav.* 62: 485–494.
- Sprague, D. S. (1998). Age, dominance rank, natal status, and tenure among male macaques. *Am. J. Phys. Anthropol.* 105: 511–521.
- Takahata, Y., Huffman, M. A., Suzuki, S., Koyama, N., and Yamagiwa, J. (1999). Why dominants do not consistently attain high mating and reproductive success: a review of longitudinal Japanese macaque studies. *Primates* 40: 143–158.
- Taub, D. M. (1980). Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus*, L.). In Lindburg, D. G. (ed.), *The Macaques: Studies in Ecology, Behaviour and Evolution*, Van Nostrand Reinhold, New York, pp. 287–344.
- Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In Aureli, F., and de Waal, F. B. M (eds.), *Natural Conflict Resolution*, University of California Press, Berkeley, pp. 106–128.
- van Noordwijk, M. A., and van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates* 40: 105–130.
- von Segesser, F. M. (1999). *Conservation Genetics of Barbary Macaques (Macaca sylvanus)*, PhD thesis, University of Zurich, Zurich.
- von Segesser, F. M., Ménard, N., Gaci, B., and Martin, R. D. (1999). Genetic differentiation within and between isolated Algerian subpopulations of Barbary macaques (*Macaca sylvanus*): Evidence from microsatellites. *Mol. Ecol.* 8: 433–442.
- von Segesser, F. M., Scheffrahn, W., and Martin, R. D. (1995). Parentage analysis within a semi-free-ranging group of Barbary macaques *Macaca sylvanus*. *Mol. Ecol.* 4: 115–120.
- Walters, J. R., and Seyfarth, R. M. (1987). Conflict and cooperation in primate societies. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 306–317.