

Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*)

Marie Charpentier,^{a,b} Patricia Peignot,^b Martine Hossaert-McKey,^a Olivier Gimenez,^a Joanna M. Setchell,^{b,c} and E. Jean Wickings^b

^aCEFE-CNRS UMR 5175, 1919 Route de Mende, 34293 Montpellier Cedex 5, France, ^bUGENET, CIRMF, Franceville, Gabon, and ^cDepartment of Biological Anthropology, University of Cambridge, Cambridge, UK

Over the last decade, paternity analysis using molecular markers has revealed that observed mating systems do not necessarily correlate with reproductive systems and thus cannot provide reliable information about male reproductive success (RS). This is especially true for primate species with a complex multimale-multifemale social organization, such as mandrills (*Mandrillus sphinx*). Using molecular markers for the measurement of individual RS and a comprehensive data set comprising 193 offspring from 27 birth cohorts over a 20-year period of sampling, we investigated the social, genetic, and demographic factors that may influence the probability of paternity by dominant male mandrills, living in a semi-free-ranging colony. We observed a significant skew in RS towards dominant males, with their probability of paternity increasing as the number of adult males in the group increased, and when they were closely related to subordinate adolescent males. Conversely, the probability of dominant males siring infants decreased when the number of simultaneously tumescent females increased. Fewer offspring were sired by dominant males when female partners were closely related to them and when the relatedness between dominant and subordinate adult males increased. These two last points suggests particularly that mechanisms of kin recognition are operating to avoid the costs of inbreeding and may also reflect the lower costs to dominant males of losing conception opportunities to more closely related subordinate adult males. This study is, to our knowledge, one of the first in primates to use an integrative approach and multivariate analysis to show that multiple factors are involved in determining the probability of paternity by dominant males. *Key words*: incest avoidance, kin recognition, mandrills, paternity analysis, reproductive skew. [*Behav Ecol* 16:614–623 (2005)]

According to sexual selection theory, dominant males should be more successful in male-male competition and mate guarding and should attract or coerce females more successfully than subordinate males (Alexander et al., 1979; Andersson, 1994; Cox and Le Boeuf, 1977). Therefore, theory predicts that the most dominant males should have the highest reproductive success (RS; Ellis, 1995). Nevertheless, environmental, demographic, and social factors, such as constraints on mate guarding, may prevent dominant males from monopolizing reproductive output (Davies, 1992). Genetic relatedness between individuals could also affect reproduction, if potentially reproductive dyads are closely related, as observed in pilot whales (*Globicephala melas*), where the two sexes remain in their natal pods for life, but all fathers are recruited from outside the pod (Amos et al., 1993).

Two current models seek to explain variation in the degree to which dominant males can monopolize reproduction within social groups. First, the “concession” model of reproductive skew proposes that dominant individuals have full control of reproduction but allow subordinates to reproduce when such reproduction brings benefits to dominants, for example, by enticing subordinates to remain and help defend the group (Kokko and Johnstone, 1999). Second, the “limited or incomplete control” model of reproductive skew proposes that subordinates will reproduce when the capacity of dominant

individuals to monopolize reproduction is reduced (Clutton-Brock, 1998). The control of reproduction is thus incomplete.

Reproductive skew and factors influencing reproductive output can only be evaluated and tested using multifactor analyses of reproductive systems combined with reliable estimates of individual contributions to successive generations. The development of molecular techniques during the last decade has revealed that behavioral measurement of mating success (i.e., frequency of copulations) does not always provide an accurate indication of male RS (i.e., number of offspring sired) because only a fraction of the total sexual activity is ever observed. The use of genetic markers has opened up the possibility of performing paternity analysis on a number of species where direct observations of mating behavior are unable to elucidate the reproductive system. In some studies, mating success estimated from observations differs from RS, with extrapair paternity, or extragroup paternity, occurring in supposedly monogamous species of birds (Griffith et al., 2002; in bluethroats *Luscinia svecica svecica*: Johnsen and Lifjeld, 2003; in common sandpiper *Actitis hypoleucos*: Mee et al., 2004), lizards (Lebas, 2001), and bats (*Saccopteryx bilineata*: Heckel and Von Helversen, 2003). Further, numerous behavioral studies of grey seals (*Halichoerus grypus*) suggest a polygynous breeding system, but a recent study showed that half of all the pups born in a colony were fathered by extragroup males (Worthington Wilmer et al., 1999). Paternity analysis therefore provides a powerful approach for the study of reproductive systems in social species.

In primate species, diversity in social organization is extreme, from male-female monogamous pairs to multimale-multifemale groups (Kappeler and van Schaik, 2002). In the

Address correspondence to M. Charpentier. E-mail: mariecharp@yahoo.fr.

Received 23 June 2004; revised 8 December 2004; accepted 17 January 2005.

latter, high-ranking males generally sire more offspring than low-ranking males (Cowlshaw and Dunbar, 1991), but studies have shown that the relationship between male rank and RS can differ at species, population, group, and even temporal levels (van Noordwijk and van Schaik, 2004). The strength of the association between rank and reproductive output depends on a number of factors. These include the ability of males to monopolize sexually receptive females, the relative success of alternative male mating strategies (e.g., in chimpanzees *Pan troglodytes*: Gagneux et al., 1999; Tutin, 1979), and the impact of female mate choice (Paul, 2002) and sperm competition, with these latter factors now appearing to be more important than previously thought (Dixson, 1998; Soltis et al., 2001). In addition, numerous life-history traits and environmental pressures affect social organization in primates, and species may respond differently to variation in these same factors. Most previous studies have examined only a limited number of offspring and/or cohorts, and hence the observed divergence in results may also be due to a lack of directly comparable situations, for example, variation in ecological or captive housing conditions.

Mandrills (*Mandrillus sphinx*, Papionini; Cercopithecinae) provide a suitable biological model in which to test hypotheses concerning RS. Mandrills are characterized by an extreme sexual dimorphism (Wickings and Dixson, 1992), suggesting a high level of intrasexual competition, and an active female mate choice (Setchell, in press). Mandrill social organization has been variously described as single-male harems, aggregations of these harems into larger groups, or multimale-multifemale hordes of hundreds of individuals (Abernethy et al., 2002; Harrison, 1988; Hoshino et al., 1984; Jouventin, 1975; Kudo, 1987; Lahm, 1986; Rogers et al., 1996), but data concerning the reproduction of wild mandrills are totally lacking due to the difficulties of studying large, itinerant hordes in dense equatorial forests.

The captive colony of mandrills at CIRMF (Centre International de Recherches Médicales de Franceville, Gabon), housed in a semi-free-ranging setting, has been studied for 20 years. Morphological and social data are routinely collected. Paternity analysis using multilocus probes of 74 offspring born between 1983 and 1994 (Wickings, 1995; Wickings et al., 1993) has shown that 70–100% of infants in a birth cohort were sired by the dominant males. Adult male mandrills mate guard estrous females (Dixson et al., 1993). The extensive longitudinal genetic data (193 offspring from 27 birth cohorts) now available for the colony at CIRMF allowed us to perform a multivariate analysis of factors influencing RS in dominant male mandrills. In this study, we present a pedigree analysis of mandrills born in the colony over a 20-year period, using microsatellite polymorphism to establish paternity.

The study had two main objectives: (1) to reexamine reproductive skew among adult male mandrills, using a larger data set and (2) to investigate the factors affecting the loss of paternity by dominant males. First, we examined demographic constraints, such as the number of males present in the group and the number of females simultaneously in estrus. Second, genetic constraints may also modulate RS, and the effects of the degree of relatedness between dominant males and reproductive females, as well as their relatedness with other males present in the group, were examined. Finally, other variables such as rank, parity, and age of reproductive females, as well as age and tenure of dominant males, may also influence the probability of paternity by dominant males. We predicted that the RS of dominant males will decrease with increased severity of these various constraints.

To our knowledge, this is one of the first primate studies to include genetic, demographic, and behavioral data in a multi-factor analysis to examine simultaneously the impact on

paternity of factors that prevent monopolization of reproduction by dominant males.

METHODS

Animals

Mandrills are semiterrestrial, forest-dwelling primates found in Gabon and adjacent areas of Equatorial Guinea, southern Cameroon, and Republic of Congo. It appears that mandrill groups are based on stable matrilineal, with female philopatry and dispersing males (Abernethy et al., 2002; Setchell et al., 2002), as in the majority of cercopithecines (Alberts and Altmann, 1995; Kuester and Paul, 1999; Pusey and Packer, 1987). The fate of dispersing males is unknown, but solitary males, estimated to be 6 years and older, have been observed. Males have never been seen to form all-male groups (Abernethy et al., 2002). Adult males are thought to be solitary or peripheral, nonpermanent members of the horde (600 individuals, up to 1000, Abernethy et al., 2002), except during the reproductive season (from June to September, corresponding to the long dry season in Gabon), when males are seen following tumescent females within the horde.

The breeding colony of mandrills at CIRMF was established in 1983–1984 when 14 unrelated animals (Wickings, 1995), originating from the wild (seven females aged 1–11 years and seven males aged 2–6 years), were released into a 6-ha rainforest enclosure (E1). Any further increases in the group have been due to natural reproduction of these founder animals, countered by deaths and some removals for experimental purposes. In 1994, in the face of an increasing population and to limit the spread of naturally occurring simian T-lymphotropic and simian immunodeficiency viruses, the colony was separated into two groups: noninfected mandrills remained in E1 ($N = 49$), and naturally infected animals were placed in E2 (3.5 ha) with all members of their matriline ($N = 21$), in order not to break kinship associations and to conserve social units.

All animals are captured annually and anaesthetized by blowpipe intramuscular injections of ketamine (Imalgène 1000; 10 mg/kg body weight). Various morphological measures and blood samples are taken on each occasion. Blood samples for DNA analysis have been collected from 1990 onwards, and hence several samples were available for analysis for the majority of individuals.

Maternity was routinely allocated from maternal behavior during the first 6 months of life until the infants were weaned, and infants were usually captured with their mothers and tattooed during these first months. Individuals older than 2 or 3 years were given colored and numbered ear tags for ease of recognition. The mandrills are provisioned twice a day with locally available fruit and monkey chow. Water is available ad libitum.

Between June 1983 and June 2002, 231 infants were born into the colony. In 2002, DNA samples from 205 individuals (81 before separation, 83 from E1, and 41 from E2 after separation), belonging to 27 cohorts, were available for analyses. Twenty-six mandrills born in the colony could not be sampled (2 stillborn, 16 died before 1 year of age, 8 never captured). The 14 founders and the 205 available offspring were included in this analysis.

Genetic analyses

DNA was extracted from whole blood or buffy coat as previously described (Wickings, 1995). DNA concentrations were measured spectrophotometrically. Samples with less than 10 µg/ml were not suitable for analysis. Of the 12 human microsatellite

loci (four base repeats) that were initially tested on colony founders, 8 were retained for paternity analysis (Table A1, Appendix A). The four other loci tested (D1S518, D11S1106, D6S271, and D6S276) were rejected as being insufficiently polymorphic or giving nonreproducible results. Two additional loci (D16S265, D6S1280) were used in two offspring, their mother and their potential sires, because the eight loci were not sufficient to discriminate between two potential fathers. The polymerase chain reaction (PCR) mixture (10 μ l) was composed of 10 mM Tris-HCl (pH 9), 50 mM KCl, 0.1% Triton X-100 (10 \times buffer), 1.5 mM MgCl₂, 0.5 μ M of each primer, 0.25 mM of each deoxynucleoside triphosphate, and 0.5 U of *Taq* DNA polymerase (Invitrogen, Cergy Pontoise, France); diluted DNA was added to give a final reaction volume of 20 μ l. Reaction conditions were as follows: initial denaturation at 94°C for 3 min, seven cycles at denaturation at 94°C for 45 s, annealing at 50°C–55°C for 1 min, and extension at 72°C for 1.5 min, followed by 30 cycles of 94°C for 45 s, 54°C–59°C for 1 min, 72°C for 1.5 min, then a final extension at 72°C for 10 min. Five microliters of each PCR product was mixed with 5 μ l of 80% formamide (0.91 g/ml) and 20% of a mix of bromophenol blue (0.25%), xylene cyanole (0.25%), sucrose (40%), and glycerol (30%), heated to 85°C–95°C for 2 min, and then loaded onto a 6% acrylamide sequencing gel (acrylamide-bisacrylamide 19:1) containing 7.5 M urea. A 100-bp DNA ladder (Invitrogen) was run adjacent to the samples to provide an absolute size marker for the microsatellite alleles. Migration took place during 3–4 h at 30–40 mA. Gels were stained using silver nitrate: gels were first immersed in pure water (10 M Ω) then washed during 20 min in a solution of 10% ethanol and 0.5% acetic acid. Gels were then stained with a solution of 0.3% silver nitrate during 10 min, rinsed with pure water, and the bands were developed in sodium hydroxide containing 0.4% formaldehyde. Finally, gels were fixed in a solution of 50% methanol and photographed before manual scoring of the genotypes.

Parentage assignment

All potential sires, 4 years or older at the time of conception (Appendix B), were genotyped for each birth cohort. Adolescent males of 4 to 9 years were considered as potential fathers because the testes descend at 3.8 years of age, marking the onset of reproductive capacity, and the first dominant male was 4 years when he first reproduced (Wickings, 1995). Jones and Ardren (2003) have suggested that CERVUS version 2.0 (Marshall et al., 1998; Slate et al., 2000) is the most accurate program to reconstruct pedigrees. Thus, paternity assignment, allele frequencies, observed and expected heterozygosities, tests of Hardy-Weinberg equilibrium, and null allele estimates were performed using CERVUS. This program calculates paternity inference likelihood ratios and generates a statistic, Δ , defined as the difference in positive log-likelihood ratios (LOD) between the two most probable candidate fathers. CERVUS uses a simulation based on the observed allele frequencies, taking into account typing error rates and incomplete sampling, to determine the statistical significance of the Δ value generated for each paternity and also includes a subroutine that calculates exclusion probabilities. To represent scoring errors, we used the default rate of 2.4%, obtained from the error rate between known mothers and offspring, and 0.926 as the mean proportion of loci typed. The statistical significance of Δ was determined at two confidence levels (CL), relaxed (80%) and strict (95%), using 10,000 simulation cycles. Results of paternity assignment by CERVUS were compared with those generated by PARENTE software (Cerueuil et al., 2002), in cases where sires were initially attributed at a relaxed level, in order to confirm results found

by CERVUS. PARENTE uses a Bayesian method, in which the posterior predictive probability of paternity is calculated for each father using information from all possible sires in the population. For each offspring, PARENTE determines a set of potential triads (offspring, mother, father) based on birth and death dates and on the allelic frequencies, the sampling rate, and the error rate and then checks the genetic and age compatibilities for all triads. Parameters used for analyses were age difference between offspring and potential mothers/fathers (3 and 5 years, respectively) and maximal delay between the birth of the offspring and the death of the female/male (0 years each). Note that PARENTE was only used in this study to assign sires as the dam's genetic identity was always confirmed by exclusion analysis. Estimates of the error rate in the data and mean proportion of loci typed were the same as for CERVUS (2.4% and 0.926, respectively).

Relatedness coefficients

All the 14 founders of the CIRMF colony were unrelated (Wickings, 1995). IBD (identical by descent) coefficients of relatedness were calculated first for each pair of potential mates (a dam and a given dominant male) for each of the 193 potential conceptions (Blouin, 2003). We then calculated a mean relatedness coefficient for dyads composed of a given dominant male and all other adult and adolescent males present in the group for each of the 193 conceptions. Thus, with the IBD method, the relatedness coefficient (R) between parent-offspring or full-sibs is 0.5.

Behavioral measures

Male and female ranks were routinely monitored using ad libitum observations of the outcome of agonistic and approach-avoidance interactions. Dominant males were assigned rank 1. However, detailed longitudinal rank data were unavailable for subordinate adult and adolescent males, which were hence all assigned the rank of 2, due to the numerous changes in their hierarchy (from day to day for some periods). For female founders and their ensuing matriline, hierarchy was matrilineal and stable, and a female's rank was expressed as the percentage of females more than 3 years of age dominated to account for demographic changes over time. All other data, including dates of birth of all individuals and mortality records, were collected routinely from the beginning of the colony.

Sexual swellings

Data on female cycles (number of cycles, stage of tumescence, number of days overlap with other maximally tumescent females, and number of tumescent females) were available only for the majority of offspring conceived during breeding seasons 1991–1994 and 1996–2001. We used daily records of females' genital swellings as visible indicators of the female hormonal cycle. Studies of other species (reviewed by Dixon, 1998) have shown that an increase in sexual swelling size co-occurs with increasing estrogen levels during the follicular phase of the menstrual cycle, and ovulation is presumed to occur during the last few days of maximal tumescence, although it may not be limited to this period. A rapid decrease in sexual swelling size (breakdown), followed by detumescence, coincides with a postovulatory rise in progesterone. For purposes of this study, the periovulatory period was defined as the 5 days preceding breakdown (Schaikh et al., 1982; Wildt et al., 1977).

Statistical analyses

Wilcoxon signed-rank tests, Mann-Whitney tests (two-tailed, $\alpha = 0.05$), and χ^2 tests (corrected for small sample size, when necessary) were used for this study; all performed with Statbox 6.3.

Repeated-measures logistic regression was used to model the relationship between the response variable (reproduction with the dominant male = 1; reproduction with a subordinate male = 0) and several explanatory variables as defined below (SAS 2001, Genmod procedure). The repeated variable was the identity of the dominant male throughout his dominance period. The method of generalized estimating equations was used to account for correlations among reproductive events of the same male. We used the backward model selection procedure (Burnham and Anderson, 1998) to select a set of explanatory variables. Initially, all the predictors were included in the model. We then removed the predictor with the highest p value greater than a cutoff fixed here at 5%, refitted the model, and repeated these steps until all p values were less than the cut off. We performed this selection procedure with three different correlation structures to ensure that our findings were robust. Selected models and estimates were found to be similar in all cases.

In order to investigate factors that influence the paternity of dominant males, we used the following variables simultaneously, corresponding to the time of conception of each offspring analyzed:

- The age, rank, and parity (primiparous versus multiparous) of the mothers as well as the relatedness coefficient mother/dominant male.
- The age and tenure (defined as the duration of dominance in the male hierarchy) of dominant males and their mean relatedness coefficient with other adult and adolescent males.
- The number of adolescent males (4–9 years old) and the number of adult males (>10 years) present at the time of conception of any given offspring.
- The number of days with more than one periovulatory female simultaneously in the group (called “overlap”). This last variable was available for 10 of the 20 years of colony history; only offspring for which all the data were available were considered (124 individuals).

RESULTS

Parentage assignment using CERVUS and PARENTE

The number of alleles per locus ranged from 6 to 16 (mean = 9.1). Expected heterozygosity (H_e) ranged from 0.671 to 0.896. CERVUS estimation of the frequency of null alleles did not reveal any deviation from Hardy-Weinberg equilibrium (Table A1, Appendix A). Overall, exclusion and likelihood analyses, using a combined CERVUS and PARENTE approach, assigned paternity for 193 of the 205 sampled animals (94.1%). CERVUS attributed a sire for 177 of 205 offspring (86.3%) with strict CL and for the remaining 28 offspring (13.7%) with relaxed CL (Table A2, Appendix A). When PARENTE was applied to the same data set, paternity was assigned with no incompatibility between the two programs in 185 cases (Table A3, Appendix A), including 170 cases with a strict CL in CERVUS. We thus accepted these 185 paternities. For 20 offspring (9.8%), incompatibilities were detected between the two programs. In three cases, sires were assigned by CERVUS with a strict CL, although the male was the second choice by PARENTE at a probability of approximately 50%; five sires were allocated by PARENTE at more than 90% CL, although the male was the second choice by CERVUS with

a relaxed CL (Table A3); 12 cases were rejected as results were either highly discordant or too weak to be reliable (four offspring were genotyped at less than four loci).

Reproductive success in male mandrills

Only 17 (34.7%) of the 49 potentially reproductively capable males in the colony (Appendix B) sired offspring. During the whole study period the nine dominant males sired 76.2% of offspring ($N = 147$) during their tenure versus 23.8% ($N = 46$) sired by the eight subordinate males. Taking into consideration these 17 successful males, the number of infants sired by dominant males during their whole tenure was significantly higher than that sired by all subordinate males during the same period (Wilcoxon signed-rank test, $N = 9$, $T = 40$, $z = 2.07$, $p < .05$).

The nine dominant males were responsible for 84.5% ($N = 163$) of the offspring sired during their tenure and during their periods as subordinate males (for $N_1 = 7$ males, Figure 1). Note that not all males that became dominant had a subordinate period before (e.g., at the beginning of the colony) or after (due to death) their tenure. Dominant males did not sire significantly more offspring during their nondominant period than other sires ($N_2 = 8$) that were never dominant (Mann-Whitney test, N_1 , N_2 , $U = 38.5$, $p = .22$) neither during the year before they acceded to the dominant position (averaged over the all subordinate males, $N = 8$, $U = 36$, $p = .64$) nor in the breeding season subsequent to their loss of dominant status, although they showed a tendency to reproduce less than other subordinate males (averaged over all subordinate males, $N = 7$, $U = 12$, $p = .1$), after loss of tenure.

Logistic regressions showed that five variables influenced the reproductive output of dominant males (Table 1). The probability of paternity by dominant males showed a negative association with the following variables: mean relatedness coefficient with other adult males, relatedness coefficient with the dam, and overlap (number of days when at least one other female was simultaneously periovulatory when the female conceived). Moreover, the probability of paternity by dominant males was positively associated with the following variables: mean relatedness coefficient with the group of adolescent males and the number of adult males present in the group. No other variable tested influenced reproductive output (Table 1).

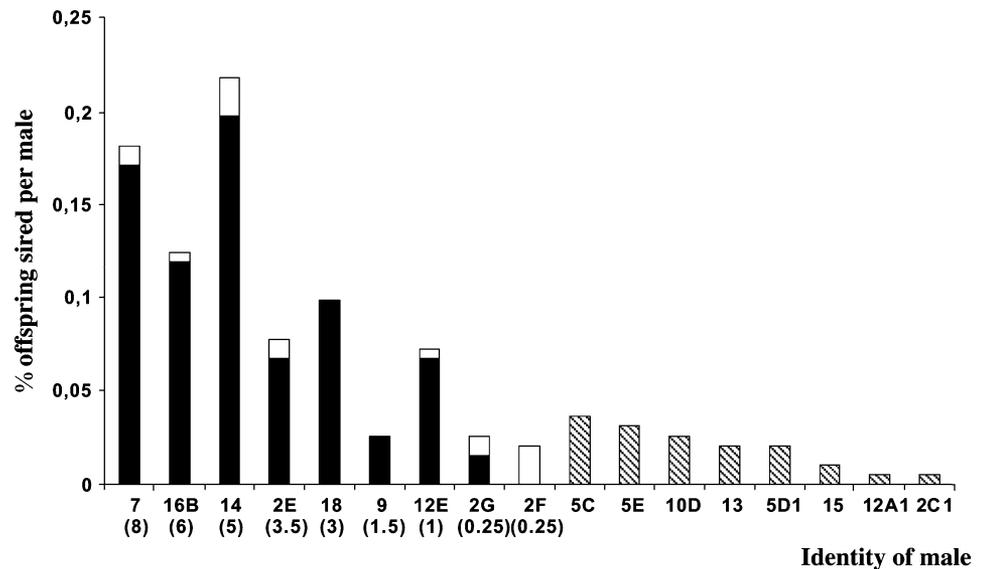
Incest avoidance

The effect of relatedness between dams and dominant males on paternity, or the avoidance thereof, was tested using χ^2 tests. For each dominant male, we calculated the percentage of offspring sired over his entire tenure, representing his “paternity rate.” Over the entire study period, potential conceptions occurred in dyads related at $R = 0$, $R = .125$, $R = .25$, $R = .313$, $R = .375$, and $R = .5$ (the highest degree of relatedness found in this study). Several dominant males were implicated in each of these categories, and the theoretical distribution of paternity was calculated from the paternity rate of each dominant male. This theoretical distribution was compared to the observed distribution of conceptions.

For five of these relatedness categories (no test was performed for the dyad related at $R = .313$ because only one case was recorded), we tested for a significant difference between the theoretical and observed distributions of conceptions, including a global test for dyads related at $R > 0$ (Table 2). Only conceptions between individuals related at $R = .5$ were significantly fewer than expected by chance. When we distinguished between mother-son, father-daughter or full-sib dyads (the three types of possible conceptions in

Figure 1

Percentage of total offspring sired by the 17 individual males with $RS > 0$. Solid bars correspond to reproductive output of dominant males during their tenure (black), and before and after tenure (white); hashed bars correspond to reproductive output of males which never become dominant; numbers in parentheses indicate the number of years of tenure for each alpha male.



dyads related at $R = .5$), too few data were available for the results to be significant. However, there was a tendency towards avoidance of potential conceptions between full-sibs (Table 2). Mean relatedness coefficients between individuals of conception dyads were significantly lower than 0.5 ($U = 81$, $N = 9$, $p < .001$). Potential conceptions between individuals related at $R = .375$ were not avoided, but the mean relatedness coefficient of the conception dyads was significantly lower than 0.375 ($U = 9$, $N = 3$, $p = .04$).

DISCUSSION

Our results showed a very high reproductive skew in male mandrills, with reproduction biased towards dominant males, but also being skewed among subordinates. This confirms previous results for the same colony (Wickings et al., 1993; Wickings 1995) for birth cohorts from 1983 to 1994, using an extensive longitudinal genetic data (1983–2002 birth cohorts).

Dominant males show the highest testosterone levels and have the most colorful sex skin (Setchell and Dixson, 2001), but once deposited, testicular volume, body mass, and red

sexual skin coloration decrease (Setchell and Dixson, 2001). Dominant males are exposed to more injurious fights in order to maintain their dominant status and when guarding potential mates than are subordinates (Charpentier, personal observation). Moreover, the effect of increasing length of tenure of dominant males, which showed a trend towards significance ($p = .07$, Table 1), was to decrease the probability of paternity by dominant males. This result is probably not due to the senescence of the dominant males as the variable “age of dominants” was not significant. These observations and results suggest that dominance engenders high costs due to maintenance of body condition and status, as well as enhanced reproductive benefits.

Nevertheless, even if dominant males are the most successful, they are not always able to monopolize reproduction, due to a number of constraints. The number of days where multiple females were simultaneously periovulatory, the number of adult males present in the group, the mean relatedness coefficient between the dominant male and the group of adolescent and adult males, and the relatedness coefficient between the dam and the dominant male all

Table 1

Effect of 11 variables on the dominant males' probability to sire offspring (logistic regression)

| Variable | Estimate | Error | <i>z</i> | <i>p</i> Value | Probability that dominant males sire offspring |
|--|----------|-------|----------|----------------|--|
| Mean <i>R</i> between the dominant male and other adult males in the group | -10.76 | 2.67 | -4.02 | <.0001 | Decreases by 10% when <i>R</i> increases by .01 |
| Mean <i>R</i> between the dominant male and adolescent males in the group | 11.95 | 2.94 | 4.07 | <.0001 | Increases by 13% when <i>R</i> increases by 0.01 |
| Overlap | -0.37 | 0.11 | -3.48 | .0005 | Decreases by 21% when overlap increases by 1 day |
| Number of adult males | 0.22 | 0.07 | 3.17 | .0015 | Increases by 25% when number of adult males increases by 1 |
| <i>R</i> between the dam and the dominant male | -3.23 | 1.05 | -3.08 | .0021 | Decreases by 28% when <i>R</i> increases by .1 |
| Tenure of dominant males | -0.19 | 0.11 | -1.82 | .07 | No significant influence on RS of dominant males |
| Rank of females | 0.01 | 0.01 | 1.24 | .21 | |
| Age of the dam | -0.02 | 0.02 | -0.90 | .37 | |
| Age of dominant males | -0.08 | 0.12 | -0.66 | .51 | |
| Parity of females | 0.41 | 0.77 | 0.53 | .60 | |
| Number of adolescent males | -0.02 | 0.11 | -0.18 | .85 | |

Table 2
 χ^2 tests on the effect of relatedness between dams and dominant males on conceptions for each relatedness category observed

| Relatedness categories | N | χ^2 | p Values |
|------------------------|-----|----------|----------|
| R = 0 | 136 | 0.14 | .71 |
| R = .125 | 13 | 0.10 | .75 |
| R = .25 | 20 | 1.95 | .16 |
| R = .375 | 4 | 0.62 | .43 |
| R = .5 | 19 | 5.07 | .02 |
| Father-daughter | 10 | 0.03 | .87 |
| Mother-son | 3 | 0 | .95 |
| Full-sibs | 6 | 2.71 | .1 |
| R > 0 ^a | 57 | 0.20 | .66 |

^a Including a dyad related at R = .313.

modulated the probability of paternity by the dominant males in this study. These results suggest that dominant male mandrills are not always able to suppress the reproductive activity of subordinates and support the limited-control model in several ways (see below).

Females simultaneously in estrus

We demonstrated that the probability of paternity by dominant males decreased with an increase in the number of days with simultaneously receptive females. Similarly, Altmann (1962) and Altmann et al. (1996) demonstrated in wild baboons that a dominant male can monopolize only one receptive female, and when two or more females are simultaneously in estrus, the second and subsequent males in the dominance hierarchy can reproduce. We were unable to test this priority-of-access model here in detail as dominance hierarchies of males were not available across the entire study period. Nevertheless, when multiple females are available, a dominant male must choose between females, as he is rarely able to guard more than one female at once; lower-ranking males have also been seen to mate guard in these situations (Dixson et al., 1993; Setchell, 1999). Preliminary behavioral data for male mandrills indicate that dominant males mate more often with high-ranking than with mid- or low-ranking females, although the dominant male does not necessarily mate guard the highest ranking female on any given day (Setchell, 1999). A more detailed examination of male mate guarding is required to address questions concerning the relationship between male dominance status, mating success, and RS in relation to the number of receptive females available.

Number of adult males in the group

A number of studies have examined the effect of the number of males on the RS of high-ranking males (Barton and Simpson, 1992; Cowlshaw and Dunbar, 1991; van Noordwijk and van Schaik, 2004), showing generally that mate guarding by the dominant male may become less effective when more males are present (Alberts et al., 2003; in macaques *Macaca sinica*: Keane et al., 1997). However, in this mandrill colony, we found the reverse, with a positive association between the number of adult males in the group and the probability of paternity by the dominant male. This surprising result may suggest that, with increasing numbers of subordinate males, which also occasionally mate guard females (Setchell, 1999), intrasexual competition between subordinates increases, deflecting competition away from the dominant male.

Relatedness between adult and adolescent males and the dominant male

The two models of reproductive skew (limited-control and concession models) make different predictions concerning the distribution of paternities among males as a function of their genetic relatedness to the dominant male. The concession model predicts that a high level of kinship among breeders will increase skew because dominant individuals allow distantly related individuals to breed as an incentive to stay in the group, that is, paternity by the dominant male decreases as relatedness between the dominant and other males decreases. On the other hand, the limited-control model predicts that close genetic relatedness has the opposite effect (Clutton-Brock, 1998), because dominant individuals are more likely to allow close relatives to reproduce, as compared to males unrelated to them. We showed that increased relatedness between a dominant male and all other adult males reduced his probability of paternity. These results suggest that there is kin recognition between close relatives in mandrills. When he is not able to control all reproductions, the dominant male may be less vigilant towards opportunistic attempts by adult male relatives than unrelated individuals (although this study does not examine the identities of subordinates that reproduced). This may reflect the lower cost to dominant males of losing paternity opportunities to more closely related subordinate males. Similarly, Widdig et al. (2004) showed in rhesus macaques that the RS of close relatives of the top sires tended to be higher than that of unrelated males. These findings appear to support the limited-control model as opposed to the concession hypothesis.

Surprisingly, in this study, we also showed that the more closely the dominant male was related to adolescent males in the group, the higher was his probability of paternity. This is the opposite of the finding concerning adult males. In the mandrill colony, different mating strategies appear to be employed at different times during a subordinate male's lifespan. A hypothetical pattern could be proposed. During adolescence, males appear to support a closely related dominant male and hence may avoid aggressive interactions that they cannot win, but on reaching adulthood, the situation is reversed and subordinate males may compete successfully for females, dominant males being less vigilant with closely related subordinates.

Relatedness, incest avoidance, and female mate choice

Mechanisms of inbreeding avoidance are well documented in vertebrate societies (Cockburn et al., 2003; Griffin et al., 2003; Mateo, 2003; Pusey and Wolf, 1996; Stow and Sunnucks, 2004; Yu et al., 2004). The main mechanism is sex-biased dispersal, generally of males, with female philopatry (Moore, 1993). Like other Cercopithecine primates, female mandrills in the CIRMF colony form clear matrilineal, with maternal inheritance of social rank (Setchell et al., 2002), while males peripheralize during adolescence (Setchell, 2003). A similar pattern is observed in wild mandrills, where males in the 6–9 years age class disappear from their natal group (Abernethy et al., 2002). However, in situations where males reintegrate into their natal group, where not all males disperse and, obviously, under captive conditions where dispersal is not possible, mechanisms of kin recognition may be important. Several studies have shown that maternal relatives avoid mating with one another (rhesus macaques: Smith, 1995; red colobus, *Procolobus badius temminckii*: Starin, 2001; Japanese macaques: Takahata et al., 2002; and see for review: Moore, 1993; van Noordwijk and van Schaik, 2004), but less is known concerning patterns of inbreeding avoidance between paternal relatives (but see

Alberts, 1999). In this study, we showed that the probability of paternity by a dominant male decreased when he was related to the dam at $R = .5$ (the highest possible relatedness coefficient in our study). Smith (1995) showed in rhesus macaques that the intensity of inbreeding avoidance was directly correlated with the closeness of kinship, as in the mandrills studied here. Among the three possible computations of conceptions between relatives with a $R = .5$, full-sibs were the only case where conceptions appeared to be avoided, suggesting that age proximity could be an important factor in the breeding patterns observed in adults (as in baboons: Alberts, 1999), as potential future breeders are likely to be close in age (mean male tenure is about 3.2 years in the colony). This result also suggests that there is an overall risk of reproduction between mother-son and father-daughter dyads, which, given the age structure of the colony and the difference in age at entry into the breeding pool of male and female mandrills, could readily occur in the colony.

The incest avoidance shown here demonstrates that female mandrills may exercise an active choice of partner, avoiding mating with close relatives, as raising an inbred offspring may be costly. A detailed study of female mate choice is indicated to determine the effects of relatedness.

Limitations of the study

The aims of this present study were to examine the variables that influence the reproductive output of dominant male mandrills under the particular conditions imposed by captivity. At this time, it is difficult to extrapolate our findings to wild conditions as very few data are available and a comparative study is not possible. The nature of the semi-free-ranging and

provisioned colony studied here could limit the interpretation of our results in several ways.

First, the males studied were unable to leave their natal group as adolescents. However, whether wild male mandrills return to their natal group to breed as adults (as in this colony) or whether they disperse and join other groups remains unknown. Moreover, adolescent males are already sexually mature at 4 years of age and may copulate before migration (Setchell et al., in press). This was observed in baboons, where males bred in their natal group before migrating (*Papio cynocephalus*: Alberts and Altmann, 1995; *Papio cynocephalus ursinus*: Bulger and Hamilton, 1988; *Papio anubis*: Packer, 1979). We thus have no reason to suppose that reproduction between close relatives would not occur in the wild.

Second, the high density of males in the colony may be an artifact of the enclosed conditions, with unrestricted breeding and low mortality. Group size reports for wild mandrills vary between 50 and 600 individuals (Abernethy et al., 2002; Jouventin, 1975; Rogers et al., 1996). Except for large hordes, where some data are now available (Abernethy et al., 2002), the annual demography of wild mandrills and the number of males present in the group on a day to day basis are unknown.

To conclude, this study shows that a combination of factors is involved in determining the reproductive output of dominant male mandrills under the captive conditions studied here. We demonstrate particularly that kin recognition occurs in the colony and that dominant males may be less vigilant when subordinate males are closely related to them, perhaps because the costs of losing paternity opportunities is lower under such circumstances. We also show incest avoidance between closely related kin, as well as the influence of other factors on paternity in males.

APPENDICES

Appendix A: genetic tables

Table A1

Characteristics of the eight microsatellite loci used for paternity analyses of 219 individuals

| Locus | Annealing temperature (°C) (7/30 cycles) | Number of alleles | Frequencies (range) | Observed heterozygosity/He | HW ^a | Null allele estimate |
|---------|--|-------------------|---------------------|----------------------------|-----------------|----------------------|
| D18S536 | 54/58 | 8 | 0.014–0.470 | 0.731/0.720 | ns | –0.0039 |
| D3S1768 | 52/56 | 10 | 0.007–0.293 | 0.798/0.812 | ns | +0.0077 |
| D12S67 | 52/56 | 16 | 0.002–0.160 | 0.939/0.896 | ns | –0.0249 |
| D13S765 | 52/56 | 8 | 0.002–0.329 | 0.819/0.773 | ns | –0.0308 |
| D8S1106 | 52/56 | 6 | 0.062–0.529 | 0.705/0.671 | ns | –0.0277 |
| D5S1457 | 52/56 | 9 | 0.005–0.289 | 0.853/0.826 | ns | –0.0172 |
| D2S1326 | 52/56 | 6 | 0.033–0.372 | 0.699/0.749 | ns | +0.0364 |
| D5S1470 | 55/59 | 10 | 0.005–0.205 | 0.899/0.866 | ns | –0.0192 |

Table A2

Results of paternity analyses from CERVUS software on 205 offspring (219 sampled animals)

| | Probability of exclusion (range) | LOD ^a (first most likely sire) | LOD ^a (second most likely sire) | Δ LOD ^b (between the two top sires) |
|------------------------------|----------------------------------|---|--|---|
| 95% Confidence ($N = 177$) | 0.998 (0.919–1) | 3.57 (0.826–7.38) | 1.04 (–2.77 to 5.54) | 2.38 (0.582–5.06) |
| 80% confidence ($N = 28$) | 0.970 (0.451–1) | 2.39 (0.665–5.68) | 2.09 (0.379–5.35) | 0.341 (0.004–0.562) |

^a LOD: the log of the product of the likelihood ratios at each locus for the most and second likely sires, respectively.

^b Δ LOD: the difference between these LODs. All values are the mean for all the individuals (range).

Table A3
Paternity allocation using CERVUS and PARENTE software

| | | CERVUS and PARENTE compatible | CERVUS and PARENTE incompatible but cases accepted |
|---------------------------|------------------------------------|-------------------------------|--|
| CERVUS, 95% confidence | Number of offspring (%) | 170 ^a (82.9%) | 3 (1.5%) |
| | LOD | 3.61 | 3.67 |
| | Probability of exclusion (CERVUS) | 0.999 | 0.999 |
| | Probability of paternity (PARENTE) | 0.837 | 0.405 |
| CERVUS, 80–95% confidence | Number of offspring (%) | 15 (7.3%) | 5 (2.4%) |
| | LOD | 2.47 | 2.29 |
| | Probability of exclusion (CERVUS) | 0.989 | 0.996 |
| | Probability of paternity (PARENTE) | 0.738 | 0.936 |

^a Including the two individuals typed at 10 loci.

Appendix B: reproductive males (potential sires) for each mating season (subsequent birth cohorts) from 4 years onwards

Table B1
Before the separation

| Breeding seasons | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 |
|-------------------------------|-------------|---------------------|-------------------------|-----------------------------|-----------------------------|---|-------------------------------------|----------------------------|---|----------------------------------|---|---|
| Adult males (+10 years) | — | — | — | — | — | 1 (3) | 3 (3, 7, 9) | 4 (7, 9, 13, 14) | 5 (<u>7</u> , 9, 13, <u>14</u> , <u>15</u>) | 6 (7, 9, 13, <u>14</u> , 15, 18) | 6 (7, 9, <u>13</u> , <u>14</u> , 15, 18) | 7 (7, 9, 13, <u>14</u> , 15, 18, 6A) |
| Adolescents males (4–9 years) | 3 (3, 7, 9) | 5 (3, 7, 9, 13, 14) | 6 (3, 7, 9, 13, 14, 15) | 7 (3, 7, 9, 13, 14, 15, 18) | 7 (3, 7, 9, 13, 14, 15, 18) | 8 (<u>7</u> , 9, <u>13</u> , 14, 15, 18, 2A, 6A) | 6 (<u>13</u> , 14, 15, 18, 2A, 6A) | 6 (15, 18, 2A, 6A, 2B, 5B) | 5 (18, 6A, 2B, 5B, 16A) | 6 (6A, 2B, 5B, 16A, 5C, 12A1) | 9 (6A, 2B, 5B, 16A, 5C, 12A1, 2E, 12E, 16B) | 11 (16A, 5C, 12A1, 2E, 12E, 16B, 2C1, 2F, 10D, 12F, 5E) |

Dominant males are in bold type; subordinate males that reproduced are underlined.

Table B2
Right enclosure (E1)

| Breeding seasons | 1994 | 1995 | 1996 | 1997 | 1998 | 2000 | 2001 |
|-------------------------------|---|--|---|---|--|---|--|
| Adult males (+10 years) | 1 (18) | 1 (18) | 1 (18) | 3 (18, <u>5C</u> , 12A1) | 5 (18, <u>5C</u> , <u>12A1</u> , 2E , 12E) | 7 (<u>5C</u> , 12A1, 2E , <u>12E</u> , <u>2C1</u> , <u>5E</u> , 2F) | 7 (<u>5C</u> , 12A1, 2E, 12E , <u>5E</u> , <u>2F</u> , 2G) |
| Adolescents males (4–9 years) | 8 (<u>5C</u> , 12A1, 2E, <u>12E</u> , 2C1, 5E, 2F, 2G) | 11 (5C, 12A1, 2E, 12E, 2C1, 5E, 2F, 2G, 2H, 2D1, 12C1) | 12 (5C, 12A1, <u>2E</u> , 12E, 2C1, 5E, 2F, 2G, 2H, 2D1, 12C1, 5D1) | 11 (2E , 12E, 2C1, 5E, <u>2F</u> , 2G, 12C1, 5D1, 10H, 12A6, 12J) | 10 (2C1, <u>5E</u> , 2F, 2G, 12C1, 5D1, 10H, 12A6, 12J, 2D3) | 13 (2G, 12C1, <u>5D1</u> , 10H, 12A6, 12J, 2D3, B, T, 12L, 5D2, 10J, 5K) | 16 (12C1, 5D1, 10H, 12A6, 12J, 2D3, B, T, 12L, 5D2, 10J, 5K, 5L, A, C, 2C4A) |

Dominant males are in bold type; subordinate males that reproduced are underlined.

Table B3
Left enclosure (E2)

| Breeding seasons | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 |
|-------------------------------|------------------------------|------------------------------------|---------------------------------------|---------------------------------|----------------------------|----------------------------|---|---|
| Adult males (+10 years) | 5 (7, 9, 13, 14 , 15) | 4 (9 , <u>13</u> , 14, 15) | 4 (9 , 13, <u>14</u> , 15) | 3 (13, 14, 15) | 3 (13, 15, 16B) | 3 (16B , 10D, 12F) | 4 (16B , <u>10D</u> , 12F, 17C) | 4 (16B , <u>10D</u> , 12F, 17C) |
| Adolescents males (4–9 years) | 4 (16B, 10D, 12F, 17C) | 5 (16B, 10D, 12F, 17C, 17A1) | 5 (16B , 10D, 12F, 17C, 17A1) | 4 (16B , 10D, 12F, 17C) | 3 (<u>10D</u> , 12F, 17C) | 3 (17C, 17B3, 17A4) | 4 (17B3, 17A4, 17D1, 6D) | 5 (17A4, 17D1, 6D, 17C, 17A5) |

Dominant males are in bold type; subordinate males that reproduced are underlined.

We are grateful to past and present staff at the Primate Center at CIRMF for keeping records of the colony. M.C. is grateful to the CIRMF for permission to study the mandrill colony and for providing logistical support; also to Simon Ossari for his valuable technical help, to Marcel Lambrechts and Prof. Doyle McKey for their helpful advice and comments on the manuscript, and to Prof. Philippe Blot (Director of CIRMF) for his support. Comments of two anonymous referees greatly improved the manuscript. Funding was partly provided by the Royal Anthropological Institute of Great Britain and Ireland. M.C. was financed by the 'Ministère Français des Affaires Étrangères'.

REFERENCES

- Abernethy KA, White LJT, Wickings EJ, 2002. Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. *J Zool* 258:131–137.
- Alberts SC, 1999. Paternal kin discrimination in wild baboons. *Proc R Soc Lond B* 266:1501–1506.
- Alberts SC, Altmann J, 1995. Balancing costs and opportunities: dispersal in male baboons. *Am Nat* 145:279–306.
- Alberts SC, Watts HE, Altmann J, 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim Behav* 65:821–840.
- Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW, 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates, and humans. In: *Evolutionary biology and human social behavior: an anthropological perspective* (Chagnon NA, Irons W, eds). North Scituate, Massachusetts: Duxbury Press; 402–435.
- Altmann SA, 1962. A field study of the sociobiology of the rhesus monkey, *Macaca mulatta*. *Ann NY Acad Sci* 102:338–435.
- Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW, 1996. Behavior predicts genetic structure in a wild primate group. *Proc Natl Acad Sci USA* 93:5797–5801.
- Amos B, Schlotterer C, Tautz D, 1993. Social structure of pilot whales revealed by analytical DNA profiling. *Science* 260:670–672.
- Andersson M, 1994. *Sexual selection*. Princeton: Princeton University Press.
- Barton RA, Simpson AJ, 1992. Does the number of males influence the relationship between dominance and mating success in primates? *Anim Behav* 44:1159–1161.
- Blouin MS, 2003. DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends Ecol Evol* 18:503–511.
- Bulger J, Hamilton WJ, 1988. Inbreeding and reproductive success in a natural chacma baboon *Papio cynocephalus ursinus* population. *Anim Behav* 36:574–578.
- Burnham KP, Anderson DR, 1998. *Model selection and inference*. New York: Springer-Verlag.
- Cercueil A, Bellemain E, Manel S, 2002. Parente: a software package for parentage analysis. *J Hered* 93:458–459.
- Clutton-Brock TH, 1998. Reproductive skew, concessions and limited control. *Trends Ecol Evol* 13:288–292.
- Cockburn A, Osmond HL, Mulder RA, Green DJ, Douvle MC, 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. *J Anim Ecol* 72:189–202.
- Cowlshaw G, Dunbar RIM, 1991. Dominance rank and mating success in male primates. *Anim Behav* 41:1045–1056.
- Cox CR, Le Boeuf BJ, 1977. Female incitation of male competition: a mechanism in sexual selection. *Am Nat* 111:317–335.
- Davies NB, 1992. *Dunnock behaviour and social evolution*. Oxford: Oxford University Press.
- Dixson AF, 1998. *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings*. New York: Oxford University Press.
- Dixson AF, Bossi T, Wickings EJ, 1993. Male dominance and genetically determined reproductive status in the mandrill (*Mandrillus sphinx*). *Primates* 34:525–532.
- Ellis L, 1995. Dominance and reproductive success among nonhuman animals: a cross species comparison. *Ethol Sociobiol* 16:257–333.
- Gagneux P, Boesch C, Woodruff DS, 1999. Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Anim Behav* 57:19–32.
- Griffin AS, Pemberton JM, Brotherton PNM, McIlrath G, Gaynor D, Kansky R, O'Riain J, Clutton-Brock TH, 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav Ecol* 14:472–480.
- Griffith SC, Owens IPF, Thuman KA, 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol Ecol* 11:2195–2212.
- Harrison MJS, 1988. The mandrill in Gabon's rain forest: ecology, distribution and status. *Oryx* 22:218–228.
- Heckel G, Von Helversen O, 2003. Genetic mating system and the significance of harem associations in the bat *Saccopteryx bilineata*. *Mol Ecol* 12:219–227.
- Hoshino J, Mori A, Kudo H, Kawai M, 1984. Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. *Primates* 25:295–307.
- Johnsen A, Lifjeld JT, 2003. Ecological constraints on extra-pair paternity in the blue-throat. *Oecologia* 136:476–483.
- Jones AG, Ardren WR, 2003. Methods of parentage analysis in natural populations. *Mol Ecol* 12:2511–2523.
- Jouventin P, 1975. Observations sur la socio-écologie du mandrill. *Terre Vie-Rev Ecol A* 29:493–532.
- Kappeler PM, van Schaik CP, 2002. The evolution of primate social systems. *Int J Primatol* 23:707–740.
- Keane B, Dittus WPJ, Melnick DJ, 1997. Paternity assessment in wild groups of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka using molecular markers. *Mol Ecol* 6:267–282.
- Kokko H, Johnstone RA, 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proc R Soc Lond B* 266:571–578.
- Kudo H, 1987. The study of vocal communication of wild mandrills in Cameroon in relation to their social structure. *Primates* 28:289–308.
- Kuester J, Paul A, 1999. Male migration in Barbary macaques (*Macaca sylvana*) at Affenberg Salem. *Int J Primatol* 20:85–106.
- Lahm SA, 1986. Diet and habitat preference of *Mandrillus sphinx* in Gabon: implications for foraging strategy. *Am J Primatol* 11:9–26.
- Lebas NR, 2001. Microsatellite determination of male reproductive success in a natural population of the territorial ornate dragon lizard, *Ctenophorus ornatus*. *Mol Ecol* 10:193–203.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM, 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol* 7:639–655.
- Mateo JM, 2003. Kin recognition in ground squirrels and other rodents. *J Mammal* 84:1163–1181.
- Mee A, Whitfield DP, Thompson DBA, Burke T, 2004. Extrapair paternity in the common sandpiper, *Actitis hypoleucos*, revealed by DNA fingerprinting. *Anim Behav* 67:333–342.
- Moore J, 1993. Inbreeding and outbreeding in primates: what's wrong with "the dispersing sex"? In: *The natural history of inbreeding and outbreeding: theoretical and empirical perspectives* (Thornhill NW, ed). Chicago: The University of Chicago Press; 392–426.
- Packer C, 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim Behav* 27:1–37.
- Paul A, 2002. Sexual selection and mate choice. *Int J Primatol* 23:877–904.
- Pusey AE, Packer C, 1987. Dispersal and philopatry. In: *Primate societies* (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds). Chicago: The University of Chicago Press; 250–266.
- Pusey A, Wolf M, 1996. Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206.
- Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJT, Tutin CEG, 1996. Ten days in the life of a mandrill horde in the Lopé Reserve, Gabon. *Am J Primatol* 40:297–313.
- Schaikh AA, Celaya CL, Gomez I, Schaik SA, 1982. Temporal relationship of hormonal peaks to ovulation and sex skin deturgescence in the baboon. *Primates* 23:444–452.
- Setchell JM, 1999. *Socio-sexual development in the male mandrill (Mandrillus sphinx)* (PhD dissertation). Cambridge: University of Cambridge.
- Setchell JM, 2003. Behavioural development in male mandrills (*Mandrillus sphinx*): puberty to adulthood. *Behaviour* 140:1053–1089.

- Setchell JM, in press. Do female mandrills prefer brightly colored males? *Int J Primatol*.
- Setchell JM, Charpentier M, Wickings EJ, in press. Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*). *Behav Ecol Sociobiol*.
- Setchell JM, Dixson AF, 2001. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Horm Behav* 39:177–184.
- Setchell JM, Lee PC, Wickings EJ, Dixson AF, 2002. Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *Int J Primatol* 23:51–68.
- Slate J, Marshall TC, Pemberton J, 2000. A retrospective assessment of the accuracy of the paternity inference program CERVUS. *Mol Ecol* 9:801–808.
- Smith DG, 1995. Avoidance of close consanguineous inbreeding in captive groups of rhesus macaques. *Am J Primatol* 35:31–40.
- Soltis J, Thomsen R, Takenaka O, 2001. The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Anim Behav* 62:485–494.
- Starin ED, 2001. Patterns of inbreeding avoidance in Temminck's red colobus. *Behaviour* 138:453–465.
- Stow AJ, Sunnucks P, 2004. Inbreeding avoidance in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Mol Ecol* 13:443–447.
- Takahata Y, Huffman MA, Bardi M, 2002. Long-term trends in matrilineal inbreeding among the Japanese macaques of Arashiyama B troop. *Int J Primatol* 23:399–410.
- Tutin CEG, 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes*). *Behav Ecol Sociobiol* 6:29–38.
- van Noordwijk MA, van Schaik CP, 2004. Sexual selection and the careers of primate males: paternity concentration, dominance acquisition tactics and transfer decisions. In: Sexual selection in primates: new and comparative perspectives (Kappeler PK, van Schaik CP, eds). Cambridge: Cambridge University Press; 208–229.
- Wickings EJ, 1995. Genetic self-management in a captive colony of mandrills (*Mandrillus sphinx*) as revealed by DNA minisatellite fingerprints. *Electrophoresis* 16:1678–1683.
- Wickings EJ, Bossi T, Dixson AF, 1993. Reproductive success in the mandrill, *Mandrillus sphinx*: correlations of male dominance and mating success with paternity, as determined by DNA fingerprinting. *J Zool* 231:563–574.
- Wickings EJ, Dixson AD, 1992. Testicular function, secondary sexual development, and social status in male mandrills (*Mandrillus sphinx*). *Physiol Behav* 52:909–916.
- Widdig A, Bercovitch FB, Streich WJ, Saueremann U, Nürnberg P, Krawczak M, 2004. A longitudinal analysis of reproductive skew in male rhesus macaques. *Proc R Soc Lond B* 271:819–826.
- Wildt DE, Doyle U, Stone SC, Harrison RM, 1977. Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology and ovarian follicular development during the baboon reproductive cycle. *Primates* 18:261–270.
- Worthington Wilmer J, Allen PJ, Pomeroy PP, Twiss SD, Amos W, 1999. Where have all the fathers gone? An extensive microsatellite analysis of paternity in the grey seal (*Halichoerus grypus*). *Mol Ecol* 8:1417–1429.
- Yu XD, Sun RY, Fang JM, 2004. Effect of kinship on social behaviors in Brandt's voles (*Microtus brandti*). *J Ethol* 22:17–22.