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Consequences of a One-male Harem Reproductive System and Inbreeding in a Captive Group of *Cercopithecus solatus*

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In closed captive populations, where dispersal is not possible, kin recognition and behavioral avoidance are the only mechanisms by which closely related individuals can avoid inbreeding. In the absence of avoidance, a loss of genetic diversity is inevitable in successive generations.

*In the 1980s, the CIRMF in Gabon established a small breeding group of sun-tailed monkeys (*Cercopithecus solatus*) with 4 individuals, and subsequently 17 births have been registered. We aimed to describe via microsatellite genotyping the reproductive system in the colony of* Cercopithecus solatus*, to evaluate the loss of genetic diversity with succeeding generations, and to evaluate consequences of inbreeding depression on a measure of the lifespan reproductive success of females giving birth to inbred vs. noninbred offspring. During the 11-yr period for which data are available, only alpha males sired offspring, confirming a one-male social organization. They reproduced only during their period of tenure. Two of the 3 alpha males were responsible for all the infants born. Genetic diversity decreased and inbreeding coefficients increased with successive generations. Interbirth interval was increased following the birth of an inbred infant, indicating possible increased maternal costs of rearing inbred infants. Loss of genetic variability in this captive group of sun-tailed monkeys has led to significant inbreeding depression and*

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demonstrates the importance of male-mediated gene flow in restricted one-male harem breeding groups.

KEY WORDS: *Cercopithecus solatus*; sun-tailed monkeys; one-male group, inbreeding depression; genetic diversity.

INTRODUCTION

In primate species, genetic analyses have emphasized the discrepancy between the observed mating system and true reproductive system (Kappeler and Van Schaik, 2002). Very few genetic studies have been conducted in cercopithecine species (Melnick and Pearl, 1987; Ohsawa *et al*., 1993). Many species of *Cercopithecus* show one-male multifemale social organization (Cords 1988) but the occurrence of multimale influxes during the breeding season is increasingly being documented (Cords, 1987; 1988; 2000; Struhsaker, 1988; Carlson and Isbell, 2001; Pazol, 2003), with >1 male mating with receptive females of the group, suggesting >1 sire per cohort of offspring. The extragroup males, with or without displacement of a resident male, ensure gene flow and maintenance of genetic diversity through generations. In the absence of male turnover, long-term tenure of one male can potentially result in females reaching maturity in the presence of their sire and with ensuing inbreeding. When mechanisms for avoiding close inbreeding, such as dispersal of one or both sexes (Moore, 1993), differential rates of maturation, and kin recognition linked with behavioral avoidance (Gouzoules and Gouzoules, 1987) break down or are no longer possible, as in closed or captive populations, females mating with close kin run the risk of producing inbred offspring, or of reduced lifetime reproductive success if they delay mating. In the wild and in captivity, inbreeding depression can affect life history traits such as birth weight, survival, reproduction, and resistance to disease (Lacy *et al*., 1993; Keller and Waller, 2002; Wayne and Morin, 2004). Although its impact on population extinction rates is still controversial (Brook *et al*., 2002; Reed *et al*., 2003), the effect of loss of genetic variability on survival should also not be underestimated. In closed captive populations, the loss of genetic diversity with successive generations is unavoidable in the absence of colony management practices (Princée, 1998; Earnhardt *et al*., 2001).

DNA typing techniques using polymorphic molecular markers provide the means to characterize reproductive patterns and social organization of species in which observational data are inconclusive or difficult to obtain *in natura* (Constable *et al*., 2001). These tools can also provide useful information in terms of accurate pedigrees for the management of captive

populations in order to avoid inbreeding and its deleterious effects (Frankel and Soulé, 1981; Laikre, 1999).

The sun-tailed monkey (*Cercopithecus solatus* Harrison, 1988) is a poorly known forest guenon species, endemic to one forest in Gabon (Forêt des Abeilles: Gautier *et al*., 1986; Harrison, 1988; Brugière *et al*., 1998; Brugière and Gautier, 1999). Due to its very secretive and cryptic nature and the difficult terrain of its home range, few eco-ethological studies have been focussed on this species. As in other forest guenons (Cords, 1988; 2000), the social organization of *Cercopithecus solatus* is a one-male unit, comprising one adult male and several adult females with their young (Gautier *et al*., 1986). In lieu of field studies, much of the information on the ecology and social organization of *Cercopithecus solatus* has been acquired from observations on the only captive group of these monkeys, which is maintained in a rain forested enclosure at CIRMF (Centre International de Recherches Médicales de Franceville, Gabon). In the group, one-male organization has also been observed with prolonged male tenure (Peignot *et al*., 1999; 2002) and expulsion of maturing males to the periphery of the enclosure (Peignot, unpublished data). Since no new individual has been introduced into the group, we suspected a high degree of consanguinity in the colony. We aimed (1) to describe the reproductive system of the colony using pedigree established by microsatellite genotyping, (2) to evaluate any loss of genetic diversity with succeeding generations, (3) to evaluate consequences of inbreeding depression on one female reproductive parameter.

MATERIALS AND METHODS

Animals

The sun-tailed monkey colony was established between 1986 and 1989, when 4 individuals (2 males and 2 females, aged from 1 to 2 yr) were acquired by the CIRMF and housed in a large outdoor cage ($6 \times 7 \times 2$ m; Table I). We estimated the age of the founders from dental eruption patterns. One male (#4) was removed from the group in May 1991 and died in 1994. In 1995, 11 individuals (3 remaining founders and their offspring), were transferred to an 0.5-ha rain forested enclosure (Peignot *et al*., 1999). Shortly after transfer, one adult male (#2A) was removed from the enclosure for the treatment of injuries received from the dominant male (#1). He was replaced in the enclosure after #1 died. In June 2002, the colony numbered 12 individuals (Table I). The monkeys were provisioned twice a day with locally available fruit and monkey chow, supplemented by natural foraging; water was available *ad libitum*.

Table I. Description of the colony of *Cercopithecus solatus* to 2002

Individual	Sex	Date of birth	Deceased	Mother	Alpha male	Assigned father	Tenure of dominant males
1[a]	M	1984	8/5/95	—	—	—	From 1989 to 5/1995
2[a]	F	1985	27/7/00	—	—	—	—
3[a]	F	1988	12/96	—	—	—	—
4	M	1986	27/1/94	—	—	—	Never
2A[a]	M	20/1/89	6/1/99	2	1	1[c]	From 5/1995 to 1/1999
2B[a]	F	30/12/90	8/8/00	2	1	1[c]	—
2*C*	*M*	22/5/92	9/92	2	1	—	—
2D	*M*	10/5/93	12/96	2	1	—	—
2E[a]	F	7/11/94		2	1	1[b]	—
2F[a]	M	9/10/95		2	1	1[b]	Compete for dominance from 1/01 to 6/02
2G[a]	M	7/1/97		2	2A	2A[b]	Compete for dominance from 1/01 to 6/02
2H[a]	F	6/4/99		2	2A	2A[b]	—
2B1[a]	M	4/9/95		2*B*	1	1[b]	Compete for dominance from 1/01 to 6/02
2B2	?	28/12/98	1/99	2*B*	2A	—	—
2E1	?	19/12/01		2*E*	*unclear*	—	—
3A[a]	M	8/12/91	12/01/01[e]	3	1	1[b]	From January 1999 to January 2001
3B	*M*	19/3/93	5/12/01	3	1	—	*Never*
3C[a]	F	26/3/94		3	1	1[d]	—
3D[a]	F	1/12/95		3	2A	2A[b]	—
3C1[a]	M	8/2/99		3C	2A	2A[b]	—
3C2	*M*	5/4/02		3C	*unclear*	—	—

Notes. Italics indicate offspring not genotyped.
[a]DNA available for analysis.
[b]Sire assigned at a strict confidence level.
[c]Sire assigned at relaxed confidence level.
[d]No sire assigned via CERVUS.
[e]Individual removed from the enclosure.

Individuals were captured annually in a fenced feeding area and anaesthetized by blowpipe intramuscular injections of ketamine (Imalgène 1000; 10 mg/kg body weight) for routine health checks. Morphological measurements and blood samples are taken on each occasion.

Maternity was allocated from observations of the maternal behavior during the first months of life until the infants were weaned, and infants were usually captured with their mothers and tattooed during these first months. For some individuals, first capture took place after infants were weaned and problems of maternal identification occurred in 2 cases (#2F and #2B1; see above).

Between 1989 and 2002, 17 infants (10M, 5F, 2 sex unknown) were born into the colony. In 2002, DNA samples from 11 offspring and 3 founders which reproduced (#1, #2, and #3) were available for analysis, corresponding to cohorts born between 1989 and 1999 (Table I). Six offspring were not sampled: 2 had died before 1 yr of age, 3 have never been captured and for 1 individual, too little DNA was available for paternity analysis.

Behavioral Measures

We routinely monitored male and female hierarchies via the outcome of agonistic behavior and approach-avoidance interactions (Peignot *et al.*, 2002). We also used group association for males as an indication of social status because only alpha males were resident in the group.

Genetic Analyses

We extracted DNA from whole blood or buffy coat as previously described for mandrills (Wickings, 1995). We initially tested 11 human microsatellite loci on some individuals, 8 of which were retained for paternity analysis (Table II). The 3 other loci tested (D2S1326, D16S265, and D18S536) were not sufficiently polymorphic or gave nonreproducible results. The PCR mixture (10 μl) was composed of 10 mM Tris HCl (pH 9), 50 mM KCl, 0.1% Triton X-100 (10X buffer), 1.5 mM $MgCl_2$, 0.5μM of each primer, 0.25 mM of each dNTP and 0.5U of Taq DNA polymerase (Invitrogen). We added diluted DNA to give a final reaction volume of 20 μl. Reaction conditions were as follows: initial denaturation at 94°C for 3 min, 7 cycles of denaturation at 94°C for 45 sec, annealing at 52–54°C for 1 min and

Table II. Characteristics of the 8 microsatellite loci used for paternity analysis of 14 individuals

Locus	Annealing temp (°C) (7/30 cycles)	No. of alleles	Frequencies (range)
D3S1768	52/56	3	0.167–0.567
D5S1457	52/56	5	0.067–0.400
D6S311	53/57	3	0.214–0.571
D5S820	52/56	3	0.107–0.786
D13S765	53/57	4	0.077–0.692
D5S1470	53/57	5	0.077–0.301
D1S207	54/58	3	0.179–0.500
D14S306	52/56	5	0.077–0.375

extending at 72°C for 1.5 min, followed by 30 cycles at 94°C for 45 sec, 56–58°C for 1 min, 72°C for 1.5 min, then a final extension at 72°C for 10 min. We mixed 5 μl of each PCR product with 5 μl 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 it to 85–95°C for 2 min, and then loaded it onto a 6% acrylamide sequencing gel (Acrylamide-Bisacrylamide 19:1) containing 7.5 M urea. We ran a 100 pb DNA ladder (Invitrogen) adjacent to the samples to provide an absolute size marker for the microsatellites alleles. Migration took place during 2–3 h at 40 mA. We stained gels via silver nitrate: first we immersed gels in pure water (10 MΩ) then washed them during 20 min in a solution of 10% ethanol, 0.5% acetic acid. We then stained gels with a solution of 0.3% silver nitrate during 10 min, rinsed them with pure water, and developed the bands in sodium hydroxide containing 0.4% formaldehyde. Finally, we fixed the gels in a solution of 50% methanol, and photographed them before manually scoring the genotypes.

We assigned paternity and determined allelic frequencies via the program CERVUS version 2.0 (Marshall *et al*., 1998), which calculates paternity inference likelihood ratios and generates a statistic (Δ) defined as the difference in positive log likelihood ratios (LOD) between the 2 top candidate fathers. CERVUS uses a simulation based on the observed allelic frequencies, taking into account typing error rates and incomplete sampling, to determine the statistical significance of the Δ value generated for each paternity. We used the default rate of 1%, to represent scoring errors, even if there was no mismatch between mother and offspring, and 0.925 as the mean proportion of loci typed. We used 10000 simulation cycles to determine the statistical significance of Δ at 2 confidence levels, relaxed (80%) and strict (95%).

We described genetic diversity using expected heterozygosities (He) performed via FSTAT version 2.9.3. (Goudet, 2001; available from http://www.unil.ch/izea/softwares/fstat.html). We tested differences in expected heterozygosities per generation via nonparametric Wilcoxon signed-rank tests (one-tailed, Statbox 6.3).

Inbreeding Depression

We calculated relatedness coefficients of the 3 founders (#1, #2, and #3) via the Fortran program MER (Moment Estimate of Relatedness), based on the moments methods developed by Wang (2002). The program estimated the 2- and 4- gene relatedness coefficients between 2 individuals from codominant genetic markers. Bootstrapping over loci is used to estimate standard deviations of the coefficients. We directly calculated

inbreeding coefficients via the IBD (Identical By Descent) method for all genotyped offspring. With this method, an offspring from a father-daughter or a mother-son conception will have an inbreeding coefficient of 0.25. We used Mann-Whitney tests (one-tailed) to test an increase of the inbreeding coefficient over 3 generations.

We tested inbreeding depression on interbirth intervals (IBI), which were calculated as the number of days between the births of successive infants surviving for >6 mo. We compared IBI between females giving birth to inbred and noninbred infants, at 2 levels: IBI before the birth of an inbred offspring and IBI following the birth of an inbred offspring. We tested simultaneously the effects of maternal rank (females #2 and #2B ranking higher than females #3 and #3C), parity, and the sex of the offspring on IBI to evaluate any effect of these parameters. We used Generalized Linear Models to model the relationship between the response variable (IBI) and the explanatory variables defined above (SAS version 8, GLM procedure). We used the descending procedure, starting with all the predictors in the model, then removing the predictor with the highest p-value, refitting the model and repeating these steps until all p-values were below the significant threshold ($\alpha = 0.05$).

RESULTS

Genotype Analysis

The number of alleles per microsatellite locus ranged from 3 to 5 (mean = 3.9). Parentage analysis via CERVUS allowed us to assign correct maternity for the 2 offspring (#2F and #2B1) for which the mothers were wrongly assigned at first capture when the offspring were tattooed. All mother-offspring pairs shared at least 1 allele at each locus. We assigned sires for 8 offspring at a strict confidence level (Table I), and 2 offspring at a relaxed confidence level, but no sire could be assigned with confidence for 1 offspring (#3C). However, as only one mismatch occurred between this genotype and one potential sire, it was probably a mutation in the offspring's genotype because it was the only individual carrying the mutated allele and every potential sire had been genotyped. Therefore, male #1 was considered to be the sire, since the second potential sire had 2 mismatches. Finally, for the first 2 offspring born in the colony (#2A and #2B), 1 founder male (#4) was not genotyped but was considered a potential sire, despite its youth. We repeated statistical analyses taking into account #4's possible paternity, but the results did not change. The pedigree of the colony is shown in Fig. 1.

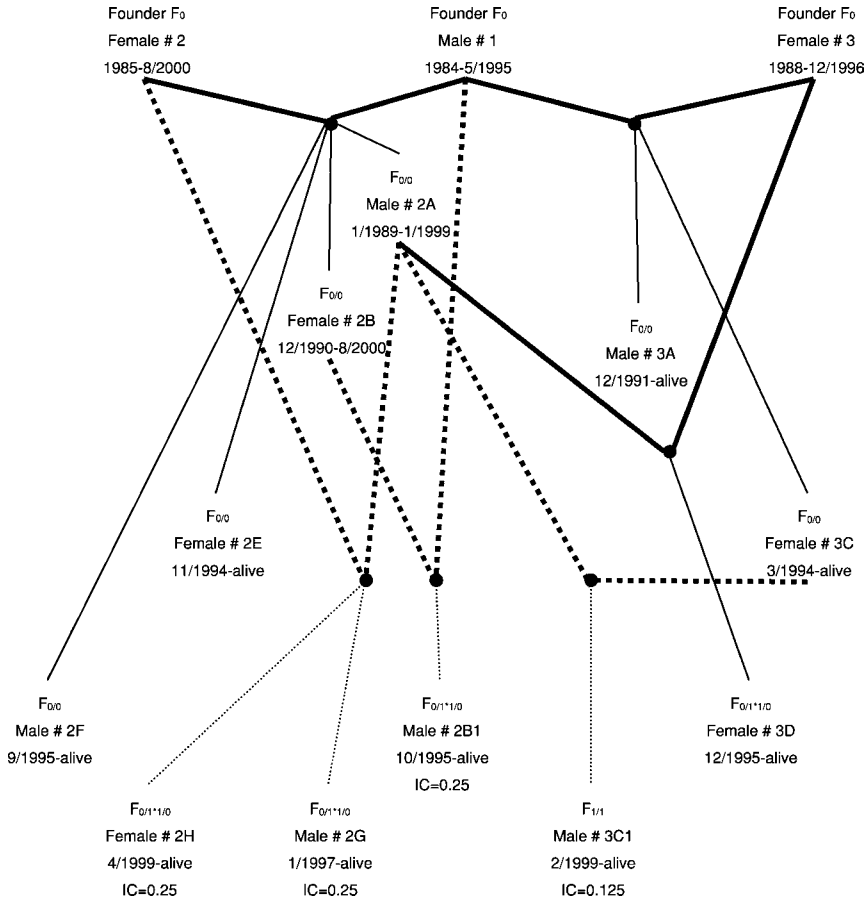

Fig. 1. Pedigree and generations of the colony of sun-tailed monkeys, showing only those offspring for which genotypes were available. Bold lines link parents. Continuous lines indicate offspring of unrelated individuals. Broken lines refer to offspring of related individuals. IC: inbreeding coefficient of the offspring.

When taking into account all 4 females that produced >1 surviving offspring (infant surviving for >6 mo), the mean reproductive rate is 0.65 offspring per year. The average rate for the 3 females for which full life histories are available is 0.54 surviving offspring per year, from the birth of their first offspring to their death. None of them showed any reduction in fecundity with increasing age (Table I).

During the 11 yr for which DNA samples were available for analysis, only 2 alpha males (#1 and #2A) reproduced out of 7 potentially reproductive males (28.6%). They were successful sires only during their alpha

tenures. Male #1 was reproductively active for 6.7 yr until his death at 11 yr, and sired ≥7 offspring (maximum 10, 3 potential offspring not sampled during his tenure). Male #2A sired ≥4 offspring during his 3-yr tenure (maximum 8, 4 potential offspring not sampled, including 1 during his tenure). One resident male (#3A) sired no offspring during his 2-yr tenure (from 1/1999 to 1/2001, Table I). After the removal of male #3A, 3 adult males (#2F, #2G, and #2B1) competed for dominance during the following 18 mo.

Loss of Genetic Diversity

Relatedness coefficients between the founder male and the 2 founder females are negative (-0.42 ± 0.11 and -0.42 ± 0.16), indicating unrelated individuals. The relatedness coefficient between the 2 founder females is 0.23 ± 0.15, indicating a possible relatedness; however, the high level of variance rendered this coefficient nonsignificant. Therefore, we considered the 3 founders as unrelated; were the 2 females related, the following results would not change. At the end of the study, 3 generations had been born in the colony. Generation $F_{0/0}$ comprised 6 individuals born to 2 founder individuals (F_0); generation $F_{0/1*1/0}$ with 4 offspring born to a founder and an individual belonging to generation $F_{0/0}$, and generation $F_{1/1}$ included 1 individual born to 2 individuals belonging to generation $F_{0/1*1/0}$. There is no evidence of avoidance of close inbreeding as the second dominant male (#2A), the son of the dominant female, reproduced successfully with all mature females in the colony during his tenure, including his mother (and assuming that he was also the father of 2B2, born during his dominance but for which no DNA was available). During the history of the colony, 4 infants were conceived following matings between relatives; 2 between a mother and her son, and 1 between a father and his daughter, giving inbreeding coefficients of 0.25. The fourth individual was born to 2 paternal half-sibs, giving an inbreeding coefficient of 0.125 (Fig. 1). Since no additional individuals have been released into the group after its creation, inbreeding increased after the first generation (between F_0 and $F_{0/0}$: Mann-Whitney tests $U = 9$, $P = 0.09$; between $F_{0/0}$ and $F_{0/1*1/0}$: $U = 6$, $P < 0.05$).

Expected heterozygosity over all loci ($N = 8$) significantly decreased between F_0 (founders) and $F_{0/0}$ (mean $He_0 = 0.76$, $He_{0/0} = 0.65$, Wilcoxon signed rank tests, $T = 31.5$, $P < 0.05$) and did not change between $F_{0/0}$ and $F_{0/1}{}^* F_{1/0}$ (mean $He_{0/1*1/0} = 0.57$, $T = 22$, $P = 0.29$).

Effects of Inbreeding on Mother Fitness

The overall interbirth interval for infants surviving >6 mo is 654 ± 296 days (mean ± sd; $N = 11$). Parity of the dam is significantly correlated

with IBI ($F = 5.56$, $P = 0.046$), primiparous females showing longer IBI (885 ± 357 days; $N = 4$) than multiparous females (521 ± 163 days; $N = 7$). The birth to an inbred offspring significantly delayed the subsequent IBI (1060 ± 212 days; $N = 3$) compared to mothers giving birth to non inbred individuals (515 days ± 131; $N = 6$; $F = 29.53$, $P < 0.001$). No other variable influenced IBI.

DISCUSSION

Our results show that only alpha males have reproduced during the history of the colony. They appear to be similar to the long-term males of *Cercopithecus ascanius* described by Struhsaker (1988), which showed a higher mating success compared to short-term tenure males. Dominance is related to paternity in *Cercopithecus solatus*, such that variance in reproductive success among males is extremely high, with only the dominant male reproducing during his alpha tenure, and a male only reproducing when dominant, to the exclusion of all other adult males. Nevertheless, dominance did not always ensure reproductive success (the case of male #3A), despite the presence of reproductive adult females without dependent young.

Nondominant males did not achieve reproductive success through opportunistic mating unlike other species, e.g. *Macaca mulatta* (Bercovitch and Nürnberg, 1997) and *Papio* spp. (Altmann and Alberts 2003). Increasing intermale competition, due to increasing numbers in the group, has led to the flight of 2 adult males from the enclosure during the last year (Peignot, unpublished data). The consequences of the one-male harem organization are an important difference in reproductive success between males, with alpha males dominating reproduction, as well as a skew between males and females. Variance in reproductive success among females is lower than in males, as all adult females had produced ≥ 1 offspring during the study period.

Inbreeding Depression in the Captive Colony

Differences in inbreeding sensitivity have been reported among primate species. Smith (1995) showed the absence of deleterious effects of inbreeding in 3 captive populations of *Macaca mulatta* for individuals with inbreeding coefficients ≤ 0.125. Conversely, in captivity, Lacy *et al.* (1993), studying inbreeding depression in a zoo population of *Callimico goeldii*, suggested that the species is particularly sensitive to inbreeding as the survival rate of female offspring of first cousin mating was only 25%, versus 75% for offspring of unrelated parents.

Sensitivity to inbreeding depression may also vary within species or even within a population (Princée, 2001; Keller & Waller, 2002). Natural populations that frequently undergo (and survive) severe bottlenecks are expected to be less sensitive to inbreeding depression than large outbred populations are (Brook *et al.*, 2002). The severity of inbreeding depression is dependent on previous events that have occurred in the population, such as the number and frequency of deleterious alleles and, therefore, on the genetic structure and history of the population (Brook *et al.*, 2002). The number of generations leading to inbreeding in small populations will depend largely on the number of unrelated founders and hence closed populations will be at risk sooner or later (Princée, 1998; Frankham, 2003). Our results from the *Cercopithecus solatus* colony show that even in early generations, genetic diversity diminishes and inbreeding depression appears to occur for mothers raising inbred offspring.

Indicators of female reproductive success are difficult to assess in the colony. Age at first birth is not informative because no inbred females have yet given birth. Fertility indicators such as ovulation and receptivity are difficult to measure in the absence of peri-ovulatory swellings and given that copulation is cryptic (Peignot, unpublished data), gestation lengths are difficult to estimate in female sun-tailed monkeys. Finally, infant mortality overall is low, perhaps due to provisioning conditions, and was not analyzed. Interbirth intervals were prolonged after the birth of an inbred infant. The maternal costs involved in successfully rearing inbred offspring may be elevated. The IBI associated with the relatedness of the subsequent male partner did not differ whether the male was related or not, suggesting that there was no active avoidance of inbreeding because females mated equally with kin and nonkin. Bearing in mind the small size of the colony and the size of the data set, it would appear that a female's reproductive success will be lowered by increased maternal investment in rearing inbred offspring rather than by avoidance of mating opportunities due to the presence of a related male. Nevertheless, given the small sample size, it was not possible to test the quality of inbred vs. noninbred offspring.

There are 2 probable causes of the actual observed consequences of inbreeding: a significant founder effect at the outset of the colony's history and the small effective population size, confounded by the social system of the species (not all adult males are reproductively active). Long-term tenure males and the one-male reproductive system of *Cercopithecus solatus* have contributed to the erosion of genetic diversity, resulting in increasing inbreeding depression.

When applied to colony management, maintenance of genetic variability implies manipulating animals to avoid inbreeding (Frankel and Soulé, 1981). The composition of breeding groups can be manipulated under

conditions *ex situ*. For optimal genetic management, maintaining separate breeding pairs is preferred to harem situations and animals living in larger colonies because this results in a larger effective population size, thus minimizing genetic loss (Princée, 1998). This restrictive practice is not appropriate for species requiring social contact or affiliative networks or both between individuals, as is the case for primates, but will ultimately depend on the housing capacity of each primate center. In the present case, the problems posed by unmanaged reproduction is the excess of males maturing to adulthood but with no possibility of migration, and hence the major policy decision must be to maintain their well-being. Secondly a decision must be taken as to whether reproduction should proceed, given the inbred nature of the individuals in the current group. A possible way to reduce the loss of genetic variability, given that the introduction of new genes through nonrelated individuals is not an option in the case of the colony of *Cercopithecus solatus*, would be to remove dominant males that are too closely related to reproductive females.

In conclusion, our data demonstrate the importance of measures to limit inbreeding in a management of small populations of this harem-forming guenon species. Although sample size is small, it cannot be increased because the colony we studied is the only captive group in existence of this rare primate. That significant effects of inbreeding, on mother reproductive success, we detected with such a small sample indicate that inbreeding depression could be strong and demonstrate the importance of male-mediated gene flow in restricted one-male harem breeding groups.

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