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Mating system and reproductive skew in the black rhinoceros

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Abstract

Only ≈ 2600 black rhinoceros survive today, mainly in small, isolated populations of < 100 animals. The management of remaining black rhinoceros populations aims at preserving natural levels of genetic relatedness and optimizing breeding success, which requires an accurate knowledge of the mating system, reproductive skew and effective population size. DNA was extracted from faecal samples from a community of 35 wild black rhinoceros, and microsatellites were used to characterize patterns of paternity of 19 offspring born from eight females in this community. Paternity could be ascribed unequivocally for each offspring. Although our conclusions must be considered tentative, we present the first genetic evidence that black rhinoceros males are polygynous, with a high variance in reproductive success. We also describe a noninvasive management tool that can be used for the genetic management of this critically endangered species, both in the wild and in captivity.

Keywords: conservation genetics, *Diceros bicornis*, dominance, likelihood, microsatellites, parentage, polygyny, reproductive success

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Introduction

The black rhinoceros (*Diceros bicornis*) has suffered one of the most dramatic declines of all mammals in recent history. There were ≈ 100 000 black rhinoceros in 1960 but numbers were reduced to ≈ 2600 in 1997, due to a major poaching onslaught linked to an increase in the demand for rhino horn (Emslie & Brooks 1999). As a result, most black rhinoceros are now distributed only in small and isolated populations located principally in four countries. Only five populations have been identified as holding > 100 animals or > 50% of a subspecies (Emslie & Brooks 1999).

Small and isolated populations are known to be vulnerable to stochastic factors. These factors can be environmental, demographic or genetic in nature and can multiplicatively threaten the continued existence of a population (Gilpin & Soulé 1986; Foose 1992). Environmental risks, such as disease epidemics and natural catastrophes, are increasingly recognized as severe threats to small populations and demographic threats (biased sex ratio, fluctuation in individual reproduction) are also a challenge for small population management (Foose & Seal 1991). Small populations may also lose genetic variability, which may be necessary for individual fitness and adaptation, through drift and inbreeding (Jiménez *et al*. 1994; Frankham & Ralls 1998; Keller 1998). Inbreeding is often associated with fitness deficit, which may further reduce the effective size of already small populations (Saccheri *et al*. 1999).

The effective size of a population is the best predictor of its ability to maintain genetic diversity. The most widely applied approach advocates that an effective population size of 50 is necessary in order to preserve populations from short-term genetic risks, whereas 500 animals is the effective population size required to maintain long-term adaptability (Soulé 1980). However, these numbers are controversial and may be an order of magnitude too small (Franklin & Frankham 1998; Lynch & Lande 1998).

For the black rhinoceros, small populations therefore need to be managed as single larger metapopulations, which may entail moving animals between subpopulations. Metapopulation management could potentially assist in the conservation of isolated subpopulations through genetic and demographic augmentation. Both wild and

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captive populations of black rhinoceros may need to be included in such a strategy because of the reduced number of each subpopulation (Emslie & Brooks 1999). The metapopulation approach is also particularly important in species with long generation times and unbalanced demographic profiles which can occur in small populations (Hanski & Gilpin 1996).

The success of conservation strategies could be enhanced by the ability to assess paternity and relatedness in black rhinoceros populations and by an accurate knowledge of their mating system. Mating systems influence relatedness levels and have large effects on effective population size (Parker & Waite 1997). However, the actual patterns of reproduction may be inconsistent with the observed patterns of reproductive behaviour in avian and mammalian mating systems, and the genetic identification of effective breeders is required for the accurate determination of reproductive success (Birkhead & Møller 1995; Amos *et al*. 1995; Fietz *et al*. 2000; Huyvaert *et al*. 2000). Such information also allows for the implementation of management procedures on the basis of accurate individual data and may also assist in optimizing breeding success in this species, thus reducing the risk of extinction.

Although much life history data are lacking, we do know that black rhinoceros are monomorphic, take 7 years to reach sexual maturity, have a gestation period of 15 months and have been suspected to be both polygynous and polyandrous (Goddard 1966; Shenkel & Shenkel-Hulliger 1969; Owen-Smith 1988). It is estimated that their reproductive life terminates at 30–35 years, whereas their life span has been reported to be ≈ 40 years in the wild (Shenkel & Shenkel-Hulliger 1969; Owen-Smith 1988). However, no empirical evidence has been collected to either confirm mating strategies or quantify their occurrence, because behavioural observations are an unreliable indicator of reproductive success in the black rhinoceros (Owen-Smith 1988). In addition, the scarcity of long-term studies that have been able to identify individual females and determine paternity in free-ranging populations has hampered the classification of female mating behaviour in rhinos, as in most mammal species (Clutton-Brock 1989).

The development of noninvasive techniques measuring steroid hormones in faeces has made the monitoring of reproductive activity in free-ranging wildlife possible (Lasley & Kirkpatrick 1991). Such a method was developed for a long-term fertility study in a wild black rhinoceros population (Garnier *et al*. 1998a,b, 2001; Garnier 2001). Parallel to this, the implementation of noninvasive genetics using faecal samples as a source of DNA has enabled the study of parentage, relatedness, population genetics and phylogeography in endangered mammals (Oka & Takenaka 1994; Constable *et al*. 1995; Gerloff *et al*. 1995, 1999; Kohn *et al*. 1995, 1999; Reed *et al*. 1997; Borries *et al*. 1999; Ernest *et al*. 2000; Fernando *et al*. 2000).

In order to augment our long-term fertility study in a wild black rhinoceros population (Garnier *et al*. 1998a, 2001; Garnier 2001), we conducted genetic analysis to determine levels of relatedness among individuals and the parentage of the progeny born during the study using microsatellites and faecal samples. The main objective of this study was to characterize the reproductive success of individual males and to investigate mating strategies in this endangered species.

Materials and methods

Study site, animals and sample collection

The study was conducted in Zimbabwe in the Save Valley Conservancy (20° E, 31° S) which is an enclosed area of 3387 km^2 dedicated to black rhinoceros conservation. A community of 35 individuals (17 males, 15 females, three unknown) was monitored between August 1995 and August 1999 in the south-eastern section of the conservancy (between Levanga/Masapas/Humani/Senuko ranches) in order to study patterns of reproductive activity in females (Garnier *et al*. 1998a, 2001; Garnier 2001). This community included 12 founders, eight of which were translocated in 1986–88, two in 1993 and another two in 1994. All founders originated from a number of locations in the Zambezi Valley. Males were considered to be adult when above 8 years of age (Hitchins & Anderson 1983; Owen-Smith 1988). In August 1999, 5 of the 11 adult males were above 20 years of age, whereas the others were all aged between 8 and 10 years.

Faecal samples were collected from all animals, except one male (Goliath, translocated in 1994), and from one calf which died at 3 weeks of age. Animals were tracked after identification of their spoor patterns and identification was further confirmed by visual observation of earnotches and natural features, such as horn length (Garnier *et al*. 1998a; Emslie & Brooks 1999). Samples were collected from the freshest dung pile left by each animal. A dung pile was considered to be fresh when the superficial layer of faecal pellets was still wet and no insect contamination had occurred. The outer layer was detached from the pellet by using a wooden stick and was inserted into a polythene bag. Samples were then dried at 65 °C for 18 h in an oven (Labotec, Johannesburg, South Africa) the same day or stored frozen until drying occurred. Dried samples were stored at 4 °C.

Consortship with males was established by observing which adult and subadult males were present with each female 15–21 months before parturition. During this period, each female was monitored every 2–3 days. Monitoring comprised locating and identifying the female, observing any interactions that she had with other individuals, recording her position using a Global Positioning System

(GPS) and the collection of a fresh faecal sample for progestagen analysis (Garnier *et al*. 1998a,b, 2001).

DNA extraction and typing

DNA extraction was carried out using the QIAamp® DNA Stool Mini Kit (QIAGEN GMBH, Hilden, Germany) and following a multiple extraction protocol, in which three extracts per faecal sample were performed (Goossens *et al*. 2000). DNA samples were dissolved in 150 µL of elution buffer and stored at –20 °C. Each sample was then processed through a multiple-tubes polymerase chain reaction (PCR; three PCR per extract) following the method of Taberlet *et al*. (1996). The best extract was always re-amplified six times in order to confirm genotypes regardless of whether individuals were homozygous or heterozygous (Taberlet *et al*. 1999; Goossens *et al*. 2000). We therefore obtained the genotype at least six times for each locus and each individual, which also helped us to solve problems of allelic dropout. Amplifications of microsatellite loci characterized previously by Brown & Houlden (1999) and Cunningham *et al*. (1999) were each carried out in 12.5 µL [10 mM Tris-HCl pH 9.0, 200 mM $(NH_4)_2SO_4$, 50 µM each dNTP, 1.5 mM $MgCl_2$, 5 ng of BSA, 0.1 U Amplitaq® Gold DNA polymerase (Perkin–Elmer), 0.5 µM non fluorescent reverse primer, 0.5 µM fluorescent (TET, FAM or HEX) forward primer, 2.5 µL of DNA extract]. A PCR amplification of 50 cycles was carried out (initial denaturation 94 °C for 10 min, 94 °C for 15 s, 49 °C to 64 °C for 30–45 s, 72 °C for 60 s). The annealing temperature was optimized for each locus (Table 1). The PCR products were visualized on a polyacrylamide gel using an ABI PRISM™ 377 DNA sequencer with GS350 Tamra marker. All gels were analysed using GENESCAN™ ANALYSIS 2.0 and GENOTYPER® 2.0 software.

Data analysis

Mother/progeny relationships were defined by behavioural observations and confirmed using genetic analysis in known progeny, except for Jaggers, Sun and Dundweri, in which maternity was established only genetically. First, parentage was assigned through standard exclusion analysis by comparing the genotypes of offspring with those of the potential fathers, knowing the genotypes of the adult female. Exclusion probabilities were calculated following the method of Chakraborty *et al*. (1988) using the program POPASSIGN, version 3.9 (SM Funk, Zoological Society of London). Cumulative exclusion probabilities across all loci were also calculated when knowing one-parent, two-parents and no-parent, respectively. Second, paternity was assessed by inclusion analysis using the program CERVUS, version 1.0 (Marshall *et al*. 1998). This program calculates the log-likelihood of each candidate parent being the true parent relative to an arbitrary individual and then calculates the difference between the two most likely parents (ΔLOD). Critical values of ΔLOD are also calculated by simulation, which incorporates a realistic rate of sampling error and removes a proportion of candidate parents to reflect the fact that not all males are sampled. Critical ΔLOD-values are generated for two scenarios: one in which both parents are unknown and one in which one parent is known. The average number of males (10) that were candidates for the paternity of each offspring was estimated from field observations. The proportion of male candidates sampled was 0.90 (all males except one were sampled). The proportion of loci typed was 100%. No mismatches were recorded between the putative mother–young pairs. However, an error rate of 1% was incorporated into the simulation. Paternity was assigned with 95% (strict) confidence level and 10 000

Table 1 Characteristics of 10 microsatellite loci typed for 33 black rhinoceros

Locus ID	Repeat size	T_a (°C), time (s)	Size (bp)	N alleles	Na freq.	H_O	H_E
*BR4**	$(CA)_{19}$	49, 45	123–131	4	−0.11	0.69	0.60
*BR6**	$(CA)_{15}$	51, 30	134–154	7	−0.02	0.81	0.80
*BR17**	$(AT)_6(GT)_{18}$	60, 30	123–135	4	−0.07	0.69	0.61
DB1†	$(CA)_{14}$	60, 30	125–129	2	−0.18	0.69	0.46
DB5†	$(CA)_{13}$	60, 45	187–205	4	−0.06	0.69	0.58
DB23†	$(CA)_{12}$	55, 30	181–183	2	−0.12	0.59	0.45
DB44†	$(CA)_4G(CA)_{16}$	64, 45	172–176	3	0.02	0.47	0.47
DB49†	$(CA)_{14}$	64, 30	154–160	4	−0.08	0.81	0.70
DB52†	$(CA)_{21}$	64, 45	214–222	5	−0.06	0.91	0.77
DB66†	$(CA)_7TA(CA)_{16}$	58, 30	189–209	5	−0.11	0.91	0.72

T_a = optimal PCR annealing temperature. Nalleles = Number of alleles per locus. Na freq = Null allele frequency per locus calculated using CERVUS, Version 1.0 (Marshall *et al*. 1998). Observed heterozygosity (H_O) and expected heterozygosity (H_E) were calculated using POPASSIGN, Version 3.9 (SM Funk, Zoological Society of London).
*Cunningham *et al*. 1999; †Brown & Houlden 1999.

paternity simulations were generated. CERVUS, version 1.0 also estimates the frequency of any null allele segregating at each locus, using an iterative algorithm based on the difference between observed and expected frequency of homozygotes. In the absence of a null allele, the estimated frequency will be close to zero, and may be slightly negative (negative values imply an excess of observed heterozygotes). Loci with high null allele frequencies (0.05 or more) should be excluded from parentage analysis (Marshall *et al*. 1998). The program also calculates the combined power of the set of loci to exclude a randomly selected unrelated candidate parent from parentage of an arbitrary offspring, given only the genotype of the offspring (total exclusionary power — first parent) and given the genotype of the offspring and of a known parent of the opposite sex (total exclusionary power — second parent), respectively.

To investigate the possibility of inbreeding, Queller & Goodnight (1989) relatedness values were also calculated for the successful pairs based on observed sample allele frequencies (Goodnight & Queller 1999) using the program POPASSIGN, version 3.9.

Results

We genotyped 19 mother–infant pairs for the 10 microsatellite loci described in Table 1. All genotypes are presented in Appendix I. The number of alleles per locus ranged from two (*DB1* and *DB23*) to seven (*BR6*). The expected heterozygosities ranged from a minimum of 0.45 (*DB23*) to a maximum of 0.77 (*DB52*). The estimated null allele frequencies are summarized in Table 1 for each locus. All values are close to zero or negative.

The results of paternity analysis are summarized in Table 2. Paternity for each of the 19 offspring could be assigned unequivocally, first because, in each case, all males except one were excluded for at least one locus. Second, the exclusion probabilities range between 0.593 and 0.999 with 15/19 values exceeding 0.950. Cumulative exclusion probabilities knowing one parent, two parents and no parent were 0.990, 0.999 and 0.920, respectively. Third, likelihood values ranged between 0.898 and 7.730 with 14/19 values exceeding 2.000; and with values twice as high as the next most likely male in 10 cases. The critical ΔLOD with 95% level of certainty was 0.26 (with 90% of the

Table 2 Paternity of 19 offspring born from eight females in a community of 35 black rhinoceros in the Save Valley Conservancy (33 individuals sampled and genotyped)

			Genetic data						Behavioural data
Mother–infant pairs						LOD score			Consortship observed 15–21 months before parturition
Mother	Offspring	Born	Genetic father	Pexcl	Nm	1st most-l	2nd most-l	ΔLOD	
Netsai* (1967)	Jete	1990	Buttom (1962)	0.980	1	2.460	0.332	2.130	
	Jaggers	1992	No Name (?)	0.593	1	2.420	1.400	1.020	
	Bonus	1995	Buttom	0.970	1	1.600	0.841	0.759	
	Boy	1997	Dundweri	0.987	2	2.520	1.800	0.721	Dundweri, Buttom, Jaggers
	84.04/S	1999	Buttom	0.983	1	2.580	0.408	2.130	Buttom, Jaggers, Bonus
Sirica (1962)	Sun	1990/91	No Name	0.616	1	2.750	0.168	2.580	
	Increase	1994	No Name	0.975	1	1.970	−0.102	1.970	
	Alice	1996	No Name	0.990	1	2.250	0.314	2.700	
Bulawayo (1962)	Dundweri	1988/89	Buttom	0.779	2	0.898	0.562	0.336	
	Mupunga	1993	Buttom	0.975	1	1.660	0.213	1.450	
	Kumalo	1996	Buttom	0.988	1	2.090	0.581	1.510	
	Chando	1998	Buttom	0.964	1	0.970	0.625	0.346	Buttom
Disco† (?)	Chiyedza	1998	Buttom	0.936	1	2.700	1.410	1.280	Buttom, Dundweri
Mazyanang (1962)	Handboy	1989	No Name	0.992	2	3.590	0.543	3.040	
Sara (1989)	Monarch	1995	Penga (1957)	0.999	1	4.260	2.400	1.860	
Jete*	Atalia	1996	Penga	0.999	4	7.730	−0.494	7.730	
	84.01/02/S	1999	Penga	0.999	2	5.560	3.180	2.390	Penga, No Name, Sun, Handboy
Harare† (1991)	Rufaro	1996	Buttom	0.988	2	3.000	−0.790	3.000	
	26.01/02/S	1998	Buttom	0.973	1	3.000	2.020	0.974	Buttom, Dundweri

Pexcl, Probability of exclusion; Nm, number of mismatches which exclude the next best father, LOD score, the log of the product of the likelihood ratios at each locus: the most likely candidate parent is the candidate parent with the highest (most positive) LOD score (1st most-l). The LOD score is also given for the second most-likely father in brackets (2nd most-l). ΔLOD is the difference in LOD scores between the most likely candidate parent and the second most likely candidate parent. Birth date for the breeding individuals (when known) is in brackets. * and † indicate a mother/daughter relationship (Netsai/Jete and Disco/Harare).

parentage resolved) if one parent was known, and 1.48 (with 68% of the parentage resolved) if neither parent was known. The total exclusionary power values (estimated by CERVUS, version 1.0), first parent and second parent, are 0.927 and 0.992, respectively.

The results indicate that among the five females that produced two or more offspring, one conceived with three different males, whereas each other female had progeny fathered by the same male. One female (Netsai) which produced five calves, had three offspring fathered by the same male (Buttom). This male also fertilized all the progeny recorded in three other females (Bulawayo: $n = 4$; Harare: $n = 2$; Disco: $n = 1$), two of which represented a mother/daughter lineage (Disco/Harare). Another female (Sirica) which produced three calves during the study bred with another male (No Name), which also reproduced successfully with two other females once (Mazyananga, Netsai). Another female (Jete), known to be the daughter of a founder (Netsai), produced two calves with a third male (Penga), also identified as having fathered an additional calf from another female (Sara).

Reproductive skew was high: 52.6% (10 of 19) of the progeny born from eight females in this community during the last 10 years can be attributed to one male (Buttom), which reproduced with four females, including a mother and daughter in the same year. Two other breeding males (Penga and No Name) reproduced alternatively and/or successively with two and three females. Until 1996, No Name and Buttom fathered an equal number of offspring. Genetic representation of Penga and No Name was 15.8% (3 of 19) and 26.3% (5 of 19), respectively, in the progeny, whereas another male (Dundweri) bred only once (5.2%). By 1999, 64% (7 of 11) of adult males had not contributed to the progeny, but five of these were only 8–10 years old. The only two males > 20 years of age that were not represented were Goliath, which had only been translocated to the study area in 1994 and had not been observed with any female, and Guy, which had been observed to consort with a female (Sara) before she produced a calf which subsequently died.

Of the five females for which consortship with males could be recorded during the 6 months preceding conception, four interacted with males (between one and three) other than those who fathered their progeny. However, three of these males were < 10 years old in 1999 (Sun, Handboy, Dundweri). Relatedness estimates within the 10 successful breeding pairs are summarized in Table 3. All values are low (negative or close to zero) suggesting that each breeding pair was unrelated.

Table 3 Relatedness values determined for the 10 successful pairs based on observed sample allele frequencies (due to Goodnight & Queller 1999) using the program POPASSIGN, Version 3.9 (SMF, The Zoological Society of London)

Breeding pairs (female/male)	Relatedness values
Netsai/Buttom	0.088
Netsai/No Name	0.020
Netsai/Dundweri	−0.361
Sirica/No Name	−0.077
Bulawayo/Buttom	−0.380
Disco/Buttom	0.195
Mazyanang/No Name	−0.261
Sara/Penga	−0.470
Jete/Penga	−0.042
Harare/Buttom	0.161

Discussion

Previous genetic studies on rhinoceros species have concerned population genetic diversity and used mitochondrial DNA (Ashley *et al*. 1990; O'Ryan & Harley 1993; O'Ryan *et al*. 1994), allozymes (Merenlender *et al*. 1989) and proteins (Swart *et al*. 1994; Swart & Ferguson 1997). Although our sample size is small and concerns only one population, the relatively high levels of observed heterozygosity are consistent with those observed by Swart & Ferguson (1997), which revealed significant differentiation between populations in Namibia and Zimbabwe. One of their main conclusions was that the Zambezi population is particularly important because of its large genetic variation. Their results indicate that the Zambezi Valley (Zimbabwe) is potentially the only remaining population containing much of the genetic variation that existed before the turn of the century (Swart *et al*. 1994; Swart & Ferguson 1997). Individuals from the Zambezi Valley population have been translocated to a number of smaller reserves in Zimbabwe (all founders of the Save Valley Conservancy population originated from the Zambezi Valley population). This could explain the high levels of genetic diversity within the community (Goossens *et al*. manuscript in preparation).

We present the first study using microsatellites extracted from faecal samples in a wild black rhinoceros population for assessing genetic relationships, and which presents genetic data and long-term behavioural observations to assess mating strategies and reproductive success. Microsatellite primers developed for the black rhinoceros successfully amplified DNA fragments using faecal samples collected in the field. Precautions were taken through multiple sampling, multiple extracting and multiple typing to obtain a reliable data set.

Through noninvasive genetic analysis and monitoring of the breeding careers of individual females over a substantial period (10 years), we have shown that one male fathered more than half of the progeny, whereas two other males fathered > 40% of offspring, providing the first genetic evidence that black rhinoceros males may be polygynous. Of those males who bred successfully, all bred

with two to four females, except for one young male, which only bred once. Polygyny and the existence of a dominance hierarchy among males, which have been found to occupy mutually exclusive territories in some studies, had been suspected previously in wild black rhinoceros (Goddard 1966; Owen-Smith 1988; Adcock 1994), but such a skew in reproductive success has not been confirmed previously. The absence of representation of other males may also possibly be attributed to their young age or their recent introduction. However, our results cannot be generalized because the study only covered a limited number of years for a long-lived species and because the population studied had been created artificially through translocation.

Polygyny is a mating system that characterizes the majority of mammalian species (Clutton-Brock 1989) and is associated with the defence of ranges or mating territories in some cervids, equids, antelopes and the white rhinoceros (Gosling 1986; Rubenstein 1986; Wemmer 1987; Owen-Smith 1988). Long-term behavioural or genetic studies are necessary to confirm differences in male breeding success (Gibson & Guinness 1980; Pemberton *et al*. 1992, 1999; Altmann *et al*. 1996; Coltman *et al*. 1998; Fietz *et al*. 2000; Huyvaert *et al*. 2000; Lebas 2001).

Comparative studies had suggested that different mating systems arise as a consequence of female dispersion, which is in turn correlated with resources distribution and predator pressure (Jarman 1974; Davies 1991). The skew in black rhinoceros male reproductive success may be associated with the spatial distribution of the animals, and may be linked to differences in fertility levels in males and/or females. Most females in this study were observed to consort with different males preceding conception, suggesting that successful fertilization might involve mate choice or sperm competition (Davies 1991). Such a situation might not be dissimilar to that of white rhinoceros, in which dominant males share territories with subordinate (or satellite) males, but have higher faecal testosterone levels, suggesting higher fertility (Owen-Smith 1988; Rachlow *et al*. 1998). It is also possible that differences in female fertility contributed to the reproductive skew observed in this study. The male that was most represented in the progeny (Buttom) was the dominant male who reproduced with half of the females. Two of these females exhibited the shortest calving interval (23 months) recorded in this population and were the most productive females, whereas two other breeding males reproduced principally with young females and subfertile females (Garnier 2001).

Another possible explanation for skew in male reproductive success could be inbreeding avoidance. In a wide variety of species, closely related individuals avoid mating with each other and there are a variety of mechanisms by which mating with familiar individuals can be avoided (Lacy *et al*. 1993; Smith 1993). In some mammal species in which daughters grow up in the presence of their father, for example common zebra (*Equus burchelli*) and feral horse (*Equus caballus*), the occurrence of female-biased dispersal and/or female reproductive suppression represents such mechanism (Berger 1986; Moore 1993; Packer & Pusey 1993).

It could not be determined in this study whether mating with relatives was avoided because the period covered was too short. All founders were unrelated (see relatedness values, Table 3), except for a mother and daughter that were translocated in 1994. Our study covered 10 years, whereas females are considered to first conceive at an average of 6–6.5 years (Adcock 1994), although an exceptional age at first conception of 3.4 years was recorded in the population (Garnier 2001). There were, however, two cases that involved a mother/daughter lineage. The mother and daughter (Disco/Harare) that were fertilized by the same male in the same year corresponded to the animals that were translocated in 1994 to the Conservancy. In contrast, the progeny of the other mother/daughter (Netsai/Jete) lineage were fathered by different males and Jete was born in the Conservancy. Interestingly, the first two females had overlapping home ranges, whereas the other two had a nonoverlapping distribution during the study (Garnier unpublished). Our sample size was too small and the study too short to conclude to any general pattern, but the occurrence of some female dispersal warrants further investigation.

Among the adult black rhinoceros males that were not represented in the progeny, five were estimated to be between 8 and 10 years old in 1999, suggesting that they may have been too young to be successful breeders. There is very little information available on age at sexual maturity in free-ranging black rhinoceros males, although they may become territorial between 8 and 10 years and subsequently begin breeding (Shenkel & Shenkel-Hulliger 1969; Adcock 1994). The finding that one young male bred successfully at ≈ 7 years of age in our study may represent an exception but data from captive animals suggest that first breeding can occur at ≈ 6 years of age (Lindemann 1982).

The dominant male in this study monopolized most of the breeding when he was between ≈ 25 and 37 years of age, which corresponds to previous observations that prime-aged males were aged between 17 and 30 years (Adcock 1994). Among the two older males (> 20 years) that were not represented in the progeny, one had only been translocated in 1994 to the Conservancy. He was not seen with any females during the study and was also reported to be very unsettled. Black rhinoceros have been reported to take at least 3 years between translocation and the establishment of their home ranges (Adcock *et al*. 1998) and this may have contributed to his absence of representation in the progeny studied. The other adult male not represented had been observed to consort with a female before she conceived her second calf. Lions killed the calf at 3 weeks and this precluded the collection of samples.

In females, we have shown that most were fertilized successfully by the same male and produced up to four calves, whereas one female reproduced with three different males. However, three of the five females that produced two calves or more had most of their progeny fathered by the dominant male. It is thus difficult to evaluate statistically how much the observation of apparent monogamy in females is in fact confounded by the skew in male reproductive success.

Goddard (1966) hypothesized that black rhinoceros might be polyandrous on the basis of mating records and our results confirm that behavioural observations are not a reliable indicator of fertilization success in this species, which can exhibit multiple mating before conception as well as post-conception mating in the wild (Shenkel & Shenkel-Hulliger 1969; Owen-Smith 1988; Garnier 2001). The reproductive life of black rhinoceros females had been estimated to last until 30–35 years, during which they are considered to be able to produce between seven and 12 calves (Shenkel & Shenkel-Hulliger 1969). Only a longer term study would be able to establish female mating strategies in this species.

More generally, we were able to determine paternity and relatedness between individuals in a wild black rhinoceros population. The broader application of such techniques to other populations could potentially enable the development of pedigrees for each management unit. Pedigrees are a powerful tool in genetic management to maximize the retention of genetic diversity (Ballou & Cooper 1992). This could apply to *in situ* black rhinoceros populations, which may in future need to be managed intensively for genetic and demographic purposes. An important aspect of black rhinoceros management is the regular translocation of individuals between breeding nuclei. This is undertaken in order to remove surplus animals and maintain an ecological carrying capacity that will allow optimal breeding, as well as the reintroduction of populations within their former range or the reinforcement of existing populations (Emslie & Brooks 1999). The periodic introduction of unrelated individuals is also required to reduce demographic extinction factors and delay the effects of inbreeding depression. However, the success of such strategies will depend on the accurate identification of the genetic and reproductive potential of translocated animals. This is especially important as some black rhinoceros will be translocated more than once in their lifetime and because translocations are costly exercises that can be associated with some mortality (Adcock *et al*. 1998; Brett 1998).

In this study, the description of a black rhinoceros mating system also provides important information for the reproductive management of this species, by representing the first scientific evidence on which to determine which pairing or grouping of animals represents the best reflection of its natural breeding system. The fact that one male monopolized more than half of the breeding in the wild population studied suggests that fewer dominant males are needed to sire the offspring in a group and that relatedness levels between the offpsring can be higher than a strict monogamous male–female pairing. This is important both *in situ* and *ex situ*, where reproductive output in captivity has been far less successful than in the wild and an important proportion of animals are not breeding regularly (Rookmaker 1998; Emslie & Brooks 1999).

Traditionally, black rhinoceros have been considered to be solitary animals and have been kept in pairs in captivity, with pairing occurring only during periods of sexual receptivity. A developing trend, however, is to manage more than a pair in systems of large paddocks. The finding that in the wild, males reproduce with at least two females suggests that captive breeding might need to be based on the grouping of more than one female with each male.

Similarly, a group of five animals was seen occasionally during the study, corresponding to the association of a female with her three calves and a breeding male. Large associations of black rhinoceros have been described in previous studies, in which observations of groups of between four and 13 animals have been reported (Goddard 1966; Shenkel & Shenkel-Hulliger 1969; Owen-Smith 1988). The identification of family kinship in the group of five animals observed during this study might be suggestive of the existence of a loose family structure in this species. This theory had also been suggested by Joubert & Eloff (1971) and Owen-Smith (1988), who argued that the black rhinoceros might not be as solitary as previously thought and that their social organization might not be dissimilar to that of the white rhinoceros.

In conclusion, this study provides the first genetic evidence of polygyny in the black rhinoceros and of an important skew in male reproductive success. It also describes a reliable noninvasive genetic management tool that allows the identification of breeders in wild populations of black rhinoceros and the monitoring of their genetic output. Together with the availability of a noninvasive reproductive monitoring procedure also based on faecal material, management can now be based on a knowledge of the breeding and genetic potential of black rhinoceros, both at an individual and population level. Such information is essential for developing accurate conservation strategies.

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This study is part of a long-term research project undertaken by Julie Garnier, wildlife veterinarian working with the Zoological Society of London, on black rhinoceros fertility in both wild and captive populations. Benoît Goossens is a postdoctoral research associate at Cardiff University, working on the genetic structure and mating system in a number of endangered species. Michael Bruford is head of the Biodiversity and Ecological Processes Group, Cardiff School of Biosciences, and is interested in evolutionary ecology and population genetics in threatened species.

Appendix I

Genotyping results for 33 wild black rhinoceros in the Save Valley Conservancy, for 10 microsatellite loci

ID	Sex	*BR4*	*BR6*	*BR17*	*DB1*	*DB5*	*DB23*	*DB44*	*DB49*	*DB52*	*DB66*
Netsai	f	123 123	140 146	123 133	125 129	199 201	181 183	174 174	154 158	214 216	189 203
Jete	f	123 125	140 144	123 133	125 129	187 201	181 181	174 174	154 158	216 220	199 203
Bonus	m	123 125	144 146	133 133	129 129	201 201	181 181	174 174	154 154	216 216	189 199
Boy	m	123 125	140 144	123 133	125 129	201 201	181 183	174 174	158 158	214 218	199 203
84.04/S	u	123 125	134 146	123 133	125 129	201 201	183 183	174 174	158 160	214 220	189 199
Sirica	f	123 125	140 144	123 133	125 129	187 201	181 181	174 176	154 158	214 216	199 203
Increase	f	123 125	134 144	133 133	125 129	201 201	181 183	174 176	154 158	214 216	195 199
Alice	f	125 125	134 144	133 133	125 129	201 201	181 183	174 176	154 158	216 220	195 199
Bulawayo	f	131 131	146 146	123 123	129 129	205 205	181 181	174 176	158 160	218 220	203 209
Mupunga	f	125 131	134 146	123 133	125 129	201 205	181 181	174 174	154 158	216 220	199 209
Kumalo	f	125 131	134 146	123 123	129 129	187 205	181 183	174 176	158 160	220 220	199 203
Chando	m	125 131	144 146	123 133	129 129	201 205	181 181	174 174	158 160	216 220	199 203
Disco	f	123 125	134 146	133 135	125 129	187 201	181 183	172 174	154 160	216 222	189 195
Harare	f	123 125	134 134	133 135	129 129	187 201	181 183	172 174	156 160	216 222	189 195
CD	f	123 125	146 146	133 133	125 129	201 201	181 183	174 174	154 158	216 220	189 203
Chiyedza	f	125 125	134 144	123 135	125 129	187 201	181 183	174 174	154 160	216 222	189 199
Mazyanang	f	123 125	140 152	123 123	129 129	201 205	181 181	176 176	154 156	216 218	199 203
Handboy	m	125 125	146 152	123 123	125 129	187 201	181 183	174 176	154 156	214 216	199 199
Sara	f	125 125	134 134	123 133	129 129	187 201	181 183	176 176	154 158	214 218	195 199
Monarch	m	125 131	134 154	123 133	129 129	187 205	181 183	174 176	158 160	214 218	195 203
Atalia	f	125 131	140 150	133 135	125 129	201 205	181 181	174 174	154 160	216 222	199 199
84.01/02/S	u	125 131	144 154	133 135	125 129	201 201	181 181	174 174	154 160	214 220	199 203
Rufaro	m	125 125	134 144	123 133	129 129	187 201	181 181	172 174	154 160	216 220	189 189
26.01/02/S	u	125 125	134 144	123 135	125 129	187 201	181 183	174 174	154 160	216 222	189 199
Guy	m	123 125	140 152	123 123	125 129	201 205	181 183	172 176	154 156	214 214	199 203
Penga	m	131 131	150 154	133 135	125 129	201 205	181 181	174 174	154 160	214 222	199 203
Buttom	m	123 125	134 144	123 133	125 129	187 201	181 183	174 174	154 160	216 220	189 199
No Name	m	123 125	134 146	123 133	125 129	187 201	181 183	172 174	154 154	214 220	195 199
Magnum	m	125 131	146 146	131 133	125 129	201 201	181 181	174 176	160 160	214 216	199 203
Dundweri	m	125 131	144 146	123 133	129 129	201 205	181 183	174 176	158 160	218 220	199 203
Sun	m	125 125	134 144	133 133	125 129	201 201	181 183	174 176	154 154	214 220	195 199
Jaggers	m	123 125	146 146	123 133	125 129	199 201	181 183	174 174	154 154	214 216	199 203
Lety	m	125 129	134 152	133 133	125 129	201 201	181 181	174 176	154 158	214 218	203 203

ID, individual identity; f, female; m, male; u, sex unknown.