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Female Southern White Rhinoceros Can Select Mates to Avoid Inbreeding

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Abstract

Current management models for many endangered species focus primarily on demographic recovery, often ignoring their intrinsic ecological requirements. Across the protected area network of southern Africa, most southern white rhinoceros are managed in populations of less than 50 individuals, experiencing restricted dispersal opportunities, and limited breeding male numbers due to their exclusive home range requirements. In the absence of information on the breeding structure of these populations, poor management decisions may require females to either forego a breeding opportunity or select to inbreed with close relatives. Here, we use a combination of social pedigree data together with genetic analyses to reconstruct the parentage of all 28 offspring produced in a 5-year period in a managed free-ranging southern white rhinoceros population. During this period, all breeding females (founders and first-generation daughters) had access to both a founder male (father to most of the daughters) and two recently introduced inexperienced males. We report that while founder females were more likely to breed with the founder male, their daughters, in contrast, were more likely to breed with the introduced males, thus avoiding inbreeding. However, we also found evidence of father–daughter inbreeding in this population, and contend that in the absence of choice, rather than forego a breeding opportunity, female white rhinoceros will inbreed with their fathers. We argue that to effectively conserve the southern white rhinoceros, managers need to understand the breeding structure of these small populations, particularly in terms of parentage and kinship.

Subject Area: Conservation Genomics and Biodiversity
Key words: *Ceratotherium simum simum*, genetic pedigree analysis, mate choice, microsatellites, population management

In naturally outbred populations, mating between relatives can lead to both reduced population growth rates and reduced fitness, as a consequence of the expression of deleterious recessive alleles and the loss of heterozygous advantages, in turn caused by increased homozygosity (e.g., Hedrick and Garcia-Dorado 2016; Kardos et al. 2016, 2018). Selection may therefore favor life-history strategies that minimize these inbreeding depression effects (Pusey and Wolf 1996; Keller and Waller 2002). These

strategies include the evolution of sex-specific dispersal, mate choice behavior, and selection for kin discrimination (Widdig 2007; Charlesworth and Willis 2009). On the other hand, a degree of inbreeding tolerance (Bateson 1982) characterizes a diverse range of taxa (Edmands 2007). In such species, inbreeding is predicted to occur when the costs of avoiding inbreeding exceed that of engaging in it due to, for example, high dispersal costs and rare mating opportunities (Kokko and Ots 2006; Szulkin et al. 2013). The degree of inbreeding is therefore dependent on both the proximate mating strategy and the population history of the species (Szulkin et al. 2013). Therefore, an inbreeding threshold, where the ecological benefits outweigh the evolutionary costs, is likely to be species specific and context dependent (Thornhill and Shields 1993; Leedale et al. 2020; Walker and Pusey 2020), and especially relevant to the persistence of species in increasingly anthropogenically altered landscapes.

Small, isolated populations are at particular risk of inbreeding among close relatives (Hedrick and Kalinowski 2000), due to the absence of dispersal opportunities and rare mating opportunities. Effective conservation of such populations requires extensive and ongoing knowledge of the mating system to determine possible demographic risks of inbreeding (Edmands 2007). Yet intensive management programs of many endangered species remain primarily focused on demographic recovery (e.g., Wilder et al. 2020). The recovery of Africa's southern white rhinoceros, *Ceratotherium simum simum* (SWR), from the brink of extinction at the start of the last century is a prominent example of modern wildlife conservation success (Player 1967; Emslie et al. 2019). With intensive protection and conservation efforts the species has recovered from a single remnant population of only ~50–100 individuals in the Kwazulu-Natal region of South Africa. Today, 20,000+ animals are distributed across a network of private and state protected areas in southern Africa (Emslie et al. 2019; Knight 2020) with an IUCN red-list category listed as Near Threatened (Emslie 2020). Nevertheless, the current management of SWR as a closed metapopulation allows for no natural dispersal. Many of the more than 400 separate population units contain fewer than 50 individuals (Emslie et al. 2019; Emslie 2020), with the mean number of SWR per population as low as 16 individuals (Chapman 2019). Across the network of small privately owned populations, which constitute more than 50% of SWR numbers (Emslie et al. 2019), owners exchange or sell breeding males to artificially maintain a level of geneflow. Yet knowledge of the species' mating system remains enigmatic and breeding success of translocated males unknown; observations of matings are very rare and the identification of breeding bulls is commonly assumed from dominance behavior alone (Owen-Smith 1975, 1988). While sexually receptive females associate principally with dominant territorial males (Rachlow et al. 1998; White et al. 2007), these males are not always successful in preventing younger males siring offspring before the latter establish their home ranges (Guerier et al. 2012). The consequences for management of rhinoceros are significant; exchanging males incorrectly identified as breeding bulls based on dominance behavior alone leaves the true fathers, whose lineage is already represented in the next generation, in the population (Guerier et al. 2012). Here, we use a combination of social pedigree data together with molecular analyses to assess parentage in a population where mating opportunities existed between daughters and their father. Given that extinction risk can be greatly enhanced by inbreeding (Brook et al. 2002; Frankham 2015, Whiteley et al. 2015), we argue that knowledge of SWR breeding systems is central to the successful conservation of endangered species.

Methods

We study a managed, free-ranging SWR population in the north of Namibia. The habitat is Karstveld, with vegetation dominated by *Colophospermum mopane* shrub and woodland (Guerier et al. 2012). This population was founded in 1993 with 4 females and 2 males imported from Hluhluwe-Imfolozi National Park, South Africa. In the 5-year period 2006–2010, 28 calves were born to 12 breeding females (4 founders, 8 first-generation (hereafter F1) daughters born to founder mothers on the reserve), each of whom had access to 3 breeding bulls (1 remaining founder, 2 young bulls recently introduced from Otjiwa Game Reserve, Namibia). Six of the 8 F1 females had been fathered by the remaining founder bull. The study period started at the point when we had confirmed parentage evidence that at least one of the introduced bulls had successfully sired a calf (calf born in 2006) and ended with the last gestation of which the founding bull may have been the sire (2009, calves born in 2010).

A full description of the sample collection and microsatellite genotyping methods, together with manual and computational analyses of parentage is given in Guerier et al. (2012). Briefly, historic management records were used to create individual pedigree profiles and identify candidate parents in the analysis. For all individuals, DNA was extracted from tissue samples obtained from ear notch or biopsy samples and in one case (one of the founder males) from a preserved tissue sample. Individuals were genotyped at 11 published microsatellite loci (7B, 7C, WR1, WR2, BR6, DB1, DB44, DB49, Rh7, Rh8, Rh9; see Guerier et al (2012) for full source and genotyping details). We investigated individual parentage using 2 methods; a manual assignment approach based on strict exclusion criteria together with computational assignments calculated within a likelihood framework implemented in Cervus v3.0 (Kalinowski et al. 2007). Confidence was calculated using likelihood-of-difference (LOD) scores at both 95% (strict) and 80% (relaxed) confidence levels.

The animals in this population are subject to intensive monitoring protocols by multiple daily ranger patrols, nocturnal waterhole monitoring, and camera trap image analysis. Individuals are identified by unique ear-notch marks, with several observations per month being typically recorded for each individual. To compute home range size, we grouped all observations for a calendar year, and calculated the area of the minimum convex polygon (MCP) bounding this set of points (Laver and Kelly 2008). By analyzing these annual home range records, we confirmed that each breeding female had potential access to each of the breeding bulls; in each case, over the study period, the average observed female home range (HR, 130 ± 30 km^2) incorporated each of the home ranges observed for the bulls ($HR_{founder}$: 39 km^2; $HR_{introduced1}$: 35 km^2, $HR_{introduced2}$: 26 km^2) (Figure 1). Using χ^2 statistics we assessed mate choice of the 2 female classes (founders and F1) by comparing our observed distribution of paternity against the expected distribution under random mate choice.

Results

In addition to the genotypes derived in Guerier et al. (2012) for calves born between before 2008, we added genotypes for a further 19 calves born between 2008 and 2010. Thus, a total of 28 calves were included in this study period (2006–2010). Using both manual and computational approaches, we were able to confirm the identity of both mother and father for all 28 calves with high levels of confidence. This allowed us to fully reconstruct the breeding structure
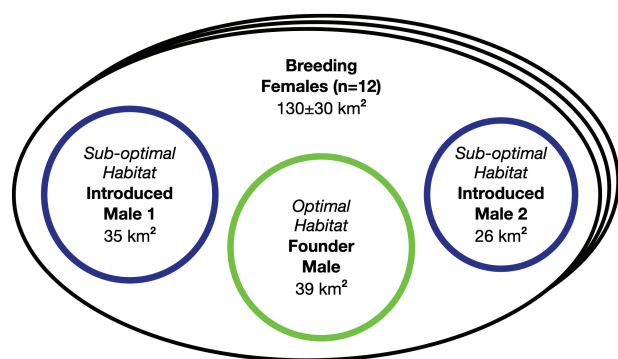
Figure 1. Schematic representation of home ranges. Shapes, shown to scale, represent the average home range size for the founder male, the introduced males and the breeding females over the 5-year study period. Males had nonoverlapping home ranges, apart from Year 1, when the introduced males were establishing their own territories. All female home ranges (mean size 130 ± 30 km², *n* = 12) incorporated each of the home ranges of the breeding males, confirming that all females had access to each of the breeding bulls. (Security considerations do not permit display of accurate geographic locations.)

over the study period (Figure 2). In the study period, the 4 founder females produced 11 calves (F1 generation) while the 8 F1 breeding females produced 17 calves (F2 generation). The founder male (D) sired 13 of the cohort of 28 calves, while the 2 introduced males sired 15 of the calves (T: 8, J: 7). Three of the 12 calves born to F1 females were the result of inbreeding with their father, founder male D, with his daughters (Di, Vi, Re). There was no significant change in the distribution of sires across the study period (Figure 2, right-hand column, $P = 0.242$, paired 2-tailed *t*-test).

We then summarized the breeding structure by grouping calf births by category of mother (founder or F1 by founder D or B) and category of father (founder or introduced) (Figure 3) and tested if the distribution was different to that expected under random mating (Table 1). Founder females were significantly more likely to breed with the founder male (9 of 11 calves born), whereas F1 females were significantly more likely to breed with the introduced males (13 of 17 calves born, $\chi^2 = 10.97$, $P < 0.001$). Two of the F1 females were sired by founder male B who was removed from the population prior to the study period, thus their breeding preferences are of particular interest. Of five calves born to these females, only one was sired by founder male D, thus these F1 females also showed a

Figure 2. Population breeding structure for the period 2006–2010, as shown by the dashed bar. Columns are grouped by matriline for the 4 founder females (OH, LH, SH, AK). For each calf and F1 female the superscript shows identity of father (D and B: founder males; T and J: introduced males). F1 female birth year shown below name and the first calf for each F1 female is underlined. Vertical bars indicate the period that each male was a possible sire. Right-hand column shows calf numbers by year, broken down by founder (f) and introduced (i) males. Calves shown by open circles are inbred by male D breeding with his daughters (calf of An in 2004 reported in Guerier et al. 2012). *Calves are not inbred; the other founder male is their grandfather. See online version for full color.

preference for the introduced males (Table 1), even in the absence of inbreeding risk.

Discussion

This study follows on from our previous work in a SWR population (Guerier et al. 2012), reporting a subsequent 5-year period where 12 breeding females (4 founders, 8 F1 daughters) had access to 3 breeding males—1 dominant founder, and 2 sub-ordinate, recently introduced individuals. Six of these daughters were sired by the same founder male, thereby creating potential for father–daughter inbreeding due to his ongoing presence on the reserve. Our parentage analysis revealed clear evidence of different breeding strategies in founder and F1 females in this highly managed population. Founder females preferred to breed with the unrelated founder male, while F1 females demonstrated inbreeding avoidance by preferring to breed with the recently introduced unrelated males.

As in our previous study (Guerier et al. 2012), we were able to assign all parents in our population using a combination of social pedigree-informed and genetic parentage analysis, while the more extensive studies of both Kretzschmar et al. (2020) and Purisotayo et al. (2019) did not achieve full pedigrees. It is likely that our complete sampling, accurate records and a small number of candidate parents, especially males, led to the greater success in parentage assignment, as these are difficult to achieve in larger longitudinal population studies (e.g., Purisotayo et al. 2019; Kretzschmar et al. 2020). Extending the available set of genetic markers, either with additional microsatellites or single nucleotide polymorphisms may

also improve assignment success in future analyses (Labuschagne et al. 2017).

In the only other genetic study of mate selection in SWR to date, Kretzschmar et al. (2020) found no evidence of inbreeding avoidance—indeed, they note that in their population, males were more likely to breed with females that were more closely related to them. In contrast, we find clear evidence of inbreeding avoidance by our F1 female offspring. We argue that the most likely reason for this difference is that we were able to explicitly assess mate selection by all our F1 females using genetic parentage analysis of a known social pedigree, rather than relying on an estimate of mean relatedness between breeding pairs to infer their pedigree relationship as in Kretzschmar et al. (2020). Relatedness measured in species in closed systems that have low genetic diversity, such as SWR, may be higher than expected for known pedigree relationships and thereby mask individual differences in breeding strategies. Kretzschmar et al. (2020) also note substantial overlap between simulated relatedness categories in their study population, suggesting some limitations to the inferred pedigree relatedness between individuals and their conclusions regarding inbreeding avoidance. Furthermore, the somewhat serendipitous extended presence of the father to most of the F1 daughters on the reserve created an ideal "experiment" for assessing mate choice by breeding females with a limited set of paternal options.

Recent studies of SWR suggest that they can discriminate between individuals based on dung odors (Cinkova and Policht 2015; Marneweck et al. 2017) and pant calls (Cinkova and Policht 2016; Cinkova and Schrader 2020; Jenikejew et al. 2020) that encode information about key traits (sex, age class, and territorial status; Marneweck et al. 2018). A role for kin discrimination in mate choice is well established for a range of species, but the strategies by which individuals are discriminated vary considerably (e.g., *chemical cues*: Archie et al. 2007 in elephant, Henkel and Setchell 2018 in chimpanzees; *home range size*: Cain et al. 2014, correlates with multilocus heterozygosity in black rhino; *vocal cues*: Leedale et al. 2020 in long-tailed tits; *genetic markers:* Green et al. 2015 in house mice).

In a wild population, female rhinoceroses disperse from the core maternal home range (Owen-Smith 1975, 1988) and roam over large areas to expose themselves to multiple territorial males, which optimizes mating opportunities (White et al. 2007). Male white rhinoceros compete for grassland-dominated territories (Owen-Smith 1975, 1988; White et al. 2007) which are also preferred female habitats (White et al. 2007), thereby increasing the probability that a female mates with the optimal territory holder. Males also try to prevent females in estrus from leaving their territory in order to further maximize mating opportunities (Owen-Smith, 1975). In our study area, given that the founder bull D occupied the prime grassland habitat, we predicted
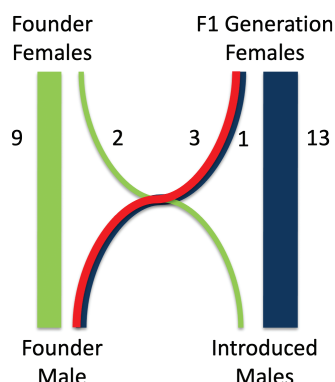

Figure 3. Distribution of parents for all 28 calves born in the period 2006–2010. Left bars are calves born to founder females (*n* = 11), right bars to F1 females (*n* = 17). Three calves are inbred (F1 daughters breeding with their founder male father).

Table 1. Distribution of calves born during the study period

| | Number of calves | | | |
| | By breeding males | | | |
By breeding females	Founder (D)	Introduced (T & J)	Total	% Sired by founder D
Founders (*n* = 4)	9	2	11	82
F1 generation (father D, *n* = 6)	3	9	12	25
F1 generation (father B, *n* = 2)	1	4	5	20

Breeding females grouped as founders or F1 generation; breeding males grouped as founder (*n* = 1, D) or introduced (*n* = 2, T & J). Founder male B was removed from the population before this study period.

that he would dominate paternity. This was the case for the founder females. However, despite their home ranges overlapping that of the founder bull, F1 females generally (76%) mated with subordinate bulls occupying suboptimal territories. We therefore believe that, apart from some young inexperienced females, male coercion did not play a major role in mate selection in our population.

Kretzschmar et al. (2020) noted that in their study population many female SWR were monogamous over their study periods. To some extent, we find similar results in our population—although we might argue that monogamy arises from mate selection, hence our founder females are in effect "monogamous" by virtue of their preference for breeding with the founder male. However, we did not record any clear preference for either introduced male by the F1 daughters. Interestingly, F1 females who did not need to avoid inbreeding (i.e., were fathered by a different founder with no known relation to founder D) also avoided the remaining founder male, although the sample size is small (*n* = 5 calves). In this population, all subadult males are removed before attaining sexual maturity, thus an age-related cue (e.g., Marneweck et al. 2018) might be sufficient to limit father–daughter inbreeding. To shed more light on this hypothesis, it would be necessary to assess mate choice in a population where related males of similar age to the females are present.

Of significant interest for the management of our study population, we have recorded 4 instances of father–daughter inbreeding. In 3 cases (see underlined open circles in Figure 2), this was the first breeding event for the female concerned, and it may be that coercion was significant for these naïve younger females, all of whom would have been mated aged 4 or 5 years (Cassini 2020). In their study populations, Kretzschmar et al. (2020) also reported an instance of father–daughter inbreeding, and Purisotayo et al. (2019) found one offspring produced by a half-sib parental pair. Together these cases provide compelling evidence that female white rhinoceros are unlikely to forego a breeding opportunity to avoid inbreeding, but that there are likely breeding strategies in place to minimize its occurrence.

Recent evidence suggests that some wild SWR populations are experiencing genetic drift (Moodley et al. 2018), which is likely to be exacerbated in smaller fenced managed populations such as ours. However, we argue that to effectively conserve SWR, managers can minimize such risks. While natural dispersal of subadult males is not possible, inbreeding can be minimized by removal of subadult males as well as breeding males after they have successfully contributed to the next generation. With few adult males with breeding potential present in a managed population, outbreeding can be optimized by ensuring that the available males represent new bloodlines. Therefore, managers need data on the breeding structure of populations, particularly focusing on parentage and kinship. This would facilitate the implementation of strategies that both promote demographic growth and maintain the genetic diversity of the species (Frankham 2015; Whiteley et al. 2015). Such plans should maximize outbreeding opportunities and avoid inbreeding where possible (Edmands 2007; Frankham et al. 2011; Ralls et al. 2018; Sánchez-Barreiro et al. 2020), including the selection of optimal candidates for translocation (Giglio et al. 2016; Purisotayo et al. 2019).

Author Contributions

K.J.S., A.S.G., and S.M.C.S. designed the research. A.S.G. and S.J.C. performed the field work. A.S.G. and A.S. performed the laboratory work. K.J.S., A.S.G., A.S., and J.M.B. analyzed data. K.J.S. and J.M.B. wrote the article. All authors reviewed and approved the article.

Data Availability

As the risk of poaching is significant in this species, the dataset (genotypes) will only be made available on explicit request.

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