Theriogenology Wild 3 (2023) 100049

Contents lists available at ScienceDirect

Theriogenology Wild

journal homepage: www.journals.elsevier.com/theriogenology-wild

The effects of animal transfers on the reproductive success of female white rhinoceroses (*Ceratotherium simum simum*) kept in European zoos

Franz Schwarzenberger *, Caroline Pannrucker

Dept. of Biomed. Sci. – Physiology, Pathophysiology & Experimental Endocrinology, Vetmeduni Vienna, 1210 Vienna, Austria

A R T I C L E I N F O

Keywords:
Southern white rhinoceros
Reproduction
Captive wildlife management
Reproductive health
Endocrine analysis

A B S T R A C T

The Southern white rhinoceros (*Ceratotherium simum simum*) has been kept in European zoos since the 1960s. However, captive breeding success has been low, with social group composition, group size, and available space all playing a role. Female rhinoceroses that have never bred or not bred for a long time have a particularly increased risk of developing reproductive tract pathologies, often resulting in infertility at a young age. One management measure to stimulate breeding is to transfer non-reproducing animals to other zoos. This study evaluated the success of transfers of 4 – 28 years old white rhinoceroses between European zoos. We analyzed n = 90 (45 males and 45 females) transfers of white rhinoceroses between 1990 and 2018. Fecal progesterone metabolite levels were analyzed for a subset of female rhinoceroses. The success of a transfer was defined as a calf born within five years. The success rate after female transfers was 26.7%; however, when the age limit of transferred females is set at 18 years, the success rate was 44.4%. The success rate after a male transfer was 23.2%. In transferred females, 83% of births occurred within three years after a transfer. Births following the arrival of a new male were distributed over five years. After a male transfer, endocrine data were determined in 26 of 82 females affected by the transfer. Positive development of estrous cycle activity after the arrival of the new bull occurred in 13 females. In summary, the success of the transfers in terms of offspring birth and endocrine stimulation of cycle activity was lower than anticipated, and sometimes a considerable amount of time elapsed before a calf was born. Nonetheless, transfers are essential to promote breeding. The relatively low success of the transfers analyzed in this study relates to the partially advanced age of the white rhinoceroses studied. Transfers of juvenile or adolescent females currently conducted between European zoos reveal a better birth rate than the present study.

1. Introduction

By the end of 2021, southern white rhinoceroses in Africa numbered approximately 16,000 individuals [1]. These in-situ populations living in national parks and on private game farms reproduce well, and there is lively trading between the different populations [2]. Rhinoceroses living in national parks are particularly threatened by poaching for the increasing demand for illegally traded rhinoceros horns. Since 2017, African white rhinoceroses have declined by 3.1% annually [1,3]. Without extensive conservation action, the white rhinoceroses could slide from "Near Threatened" to the "Endangered" category on the IUCN Red List [4] within the next few years.

Globally, zoos attempt to establish a self-sustaining ex-situ population of white rhinoceroses; this species has been kept in European zoos for about 60 years [5–9]. In a large wave of imports in the 1970s, many white rhinoceroses were imported from South Africa; however, within a decade, it became apparent that the captive rhinoceroses did not reproduce well [5–7,10,11]. The low breeding propensity of captive white rhinoceroses strongly juxtaposes with the well-reproducing population in South Africa [2,3,12]. For many years, more white rhinoceroses were imported from the wild than were born in zoos [6,7]. Only 38% of female white rhinoceroses of reproductive age in the EEP (EAZA Ex-situ Program; EAZA - European Association of Zoos and Aquaria) population ever reproduced, compared to about 98% in a wild population in Kenya [13]. In recent years, the European population has stabilized. The proportion of female white rhinoceroses in the EEP producing offspring, and thus the number of calves born annually, has slightly increased since 2000, however, to achieve a self-sustaining population, the proportion of breeding females need to increase [7].

The relatively low reproductive rate of the captive population

* Correspondence to: Veterinarmedizinische Universitat, Vienna, Austria.
E-mail address: Franz.Schwarzenberger@vetmeduni.ac.at (F. Schwarzenberger).

https://doi.org/10.1016/j.therwi.2023.100049
Received 31 March 2023; Received in revised form 26 July 2023; Accepted 6 August 2023
Available online 7 August 2023

necessitates efforts to increase breeding activity. Social factors such as group size and composition are considered major contributors to low reproductive success in captivity [8,9,13–16]. The reproductive system of white rhinoceros in the wild is characterized by a territorial mating system in which adult males defend their territory and dominate mating activities; females move freely between male territories [2,12]. Zoos attempt to simulate this social system by keeping groups of females with one or two bulls. Group sizes in European facilities range from 2 to 11 individuals [6–8]. A limiting factor for the realization of changes in group sizes and, thus, in the social system is the existing infrastructure (buildings and enclosures), which must meet animal needs and provide shelter and comfort during European winter conditions. In all three rhinoceros species kept in Europe, the best conditions for reproduction are found in the spring and summer months, and because of a 16 – 18 months gestation, this results in an accumulation of births in the autumn and winter months [17,18].

In search of the causes of low reproductive success of white rhinoceroses in captivity, extensive ultrasonography of the genital tract and endocrinological studies have been conducted in recent decades [11, 19–21]. Female white rhinoceroses that do not reproduce for a prolonged period often develop progressive reproductive pathologies, such as cystic endometrial hyperplasia, hydromucometra, leiomyomas of the cervix, uterus, and ovaries, adenomas, and para-ovular cysts. These diseases of the genital tract do not occur in animals that have had at least one pregnancy at a young age [19].

The analysis of fecal progesterone metabolites has long been used as a safe, non-invasive method for monitoring the fertility of female white rhinoceroses [22–25]. Fecal progesterone metabolites mirror both luteal and placental function and significantly correlate to plasma progesterone with a delay of approximately two days [26]. Through its examination, corpus luteum activity, gestation or miscarriages, seasonality and hormonal therapies can be monitored or studied [24,26]. This allowed detailed investigations of the estrous cycle and gestation of white rhinoceros [18]. In white rhinoceroses, two distinct cycle lengths of approximately 30–35 and 65–70 days occur [22,23]. In addition, irregular cycles, sustained luteal activity, or prolonged acyclic phases have been diagnosed in many captive white rhinoceros females [22].

At the turn of the millennium, proposals were made to overcome reproductive problems in the captive white rhinoceros population [10]. These recommendations included endocrine monitoring and the transfer of animals to promote natural reproduction. Management measures recommended explicitly by the EEP studbook for white rhinoceroses include the transfer of males or females between herds or temporary isolation of males from the female group for several months. Because subadult females leave their mothers in the wild, the EEP considers it essential to separate these subadult animals from the mother herd in captivity [6–8]. Such changes in herd structure are thought to stimulate reproduction in otherwise non-reproductive animals, although this is not the case for all females, underscoring the importance of mate choice and group composition in southern white rhinoceroses [2,13–16,27]. This study aimed to evaluate the success of animal transfers in the EEP by analyzing European and International Studbooks and hormonal results collected over almost three decades (1990–2018).

2. Material and methods

We analyzed the results of male and female white rhinoceroses transfers between European zoos between 1990 and 2018 to determine whether this could enhance captive breeding. The success of a transfer was defined as a calf born within five years involving a transferred male or female white rhinoceros. Data used for the analysis were obtained from the European White Rhinoceroses Studbooks [6,7], the 13th editions of the International White Rhinoceroses Studbook [5], and information from the Rhinos of the World (https://worldrhino.com/white-rhinos-european-zoo/) [28] and Rhinos in Europe (https://rhinos-in-europe.net) [29] websites. The EEP coordinator for white rhinoceroses, L. Versteege (Beekse Bergen), kindly provided data for transfers conducted in 2018.

In addition to the Studbook data, hormone data from female white rhinoceroses collected in the endocrine laboratory of VetMedUni Vienna over the last three decades (1991–2021) were analyzed [18]. These data were only available in some transfers, as in many cases, no fecal samples were collected, or the samples were only collected before or after the transfer. Samples analyzed were collected in a series of one to two samples per week and usually for 1–2 years. Sampling began 6–12 months (in some cases as early as 2 years) before the transfer. Samples were analyzed using a 20-oxo-pregnane enzyme immunoassay. The group-specific antibody used in this assay was prepared in rabbits against 5α-pregnane-3ß-ol-20-one 3HS:BSA, and it cross-reacts with fecal 5α- and 5β-reduced pregnane metabolites containing a 20-oxo group [22]. The analytical methods for assaying the fecal samples, including extraction, have remained the same since the methods were first introduced, thus making the results of hormone analyses readily comparable between years [18].

To assess the impact of the transfers on reproduction, we created tables for female and male white rhinoceroses based on the tabulated listings in the Studbooks [5–7]. We determined the periods when certain animals were in the same zoo at the same time; thus, we assumed that they had the opportunity to interact with each other. Transfers of males living in bachelor groups without female contacts were excluded.

The criteria for selecting the animals in our study were age and transfer history. We restricted the age range of males and females to four to 28 years, as the youngest dam was four years at first reproduction, and the oldest primiparous dams were 28 and 25 years, respectively. However, females with offspring at a young age may continue to produce calves up to about 35 years of age; males may be fertile up to about 40 years of age [7]. After a transfer of a male rhinoceros, it usually takes two months for the new bull to be introduced to the group of females in a zoo [8,9], so we highlighted zoos where the male was older than four years, and the stay was longer than two months. To select the female rhinoceroses, individual life history charts were created using the compiled tables, studbook entries and the websites mentioned above as data sources. The criteria for selection were that non-pregnant females that had not produced offspring for at least four years had either been relocated to a new zoo or had been exposed to a new male. Further investigation of the life history tables consisted of determining whether a transfer (male or female) resulted in a pregnancy and, if so, how many days elapsed between the transfer and the birth of a new calf. We set the limit for a transfer-induced birth at five years (1825 days). The results were summarized, and the percentage of pregnancies resulting from female or male transfers was calculated.

Studbook and transfer data were linked to hormone profiles for a subset of female rhinoceroses. The analysis and evaluation were performed as described in Schwarzenberger et al., 1998 [22]. The categories used in 1998 were 1) regular estrous cycles of ~10 weeks length and 20-oxo-P concentrations during the luteal phase of > 800 ng/g feces; 2) estrous cycles of ~4–10 weeks length and 20-oxo-P levels during the luteal phase of ~250–750 ng/g feces; 3) persistent luteal activity, no estrus cycle regularity, 20-oxo-P concentrations of ~ 100–200 ng/g feces; 4) lack of luteal activity ("flatliner"), 20-oxo-P concentrations < 100 ng/g feces. The change from a higher to a lower category (e.g., from 4 or 3 to a 2 or 1) was considered positive, and the other direction (e.g., from 1 or 2 to a 3 or 4) was negative. The outcome was considered neutral when the ovarian activity category did not change. In several cases, endocrine data were available only before or after transport, and these results were classified as "unknown" (not assessable).

3. Results

We analyzed studbook data of n = 740 (344 males and 396 females) rhinoceroses. Of these, 40 females and 36 males met our criteria. Some of these 76 individuals (female or male) were transferred more than once, thus, the total number included in the study was 90 (45 male and 45 female transfers).

3.1. Birth of offspring after rhinoceros transfers

The success of a transfer was defined as a calf born within five years of a transfer from one of the two parent animals. The success rate after female transfers is 26.7% (12 offspring out of 45 transfers; Table 1); however, when the age limit of transferred females is arbitrarily set at 20 years, the success rate is 37.5% (12 out of 32 transfers). The oldest female that conceived was transferred at 18 y of age. Therefore, if the age limit is set at 18 years, the success rate is 44.4% (12 out of 27 transfers).

Table 2 lists the transfers of 36 males. Some of these animals were transferred multiple times; the 36 males were paired with 65 females ranging in age from four to 28 years, resulting in 83 transfers listed in Table 2. Of the 83 pairings, 74 females were under 20 years. Within five years of the arrival of the transferred male, 19 rhinoceros calves were born (19 out of 82 new female/male combinations, a success rate of 23.2%). When comparing male and female transfers, male transfers show an earlier occurrence of success; however, female transfers had a higher overall success rate than male transfers.

The number of days between the transfer of a female or the arrival of a new bull and a resulting birth is shown in (Fig. 1). After the transfer of a female, most births (n = 10 of 12) occurred within three years of the female arrival. In contrast, births following the arrival of the new male were more evenly distributed over five years. In females #1280 and #1684, calves were born as late as 2096 and 2142 days, respectively, after the arrival of a male. These two births exceed the set time frame of five years (1825 days) but are included in the > 1700-day category in Fig. 1.

A remarkable occurrence was the transfer of 24-year-old bull #796, socialized with 26-year-old nulliparous female #767. Three years after the bull's arrival, an abortion unexpectedly occurred. Female #767 became pregnant again about three months after the abortion, and thus a female calf was born 1724 days after the bull arrived from the now 30-year-old dam. Another case of abortion occurred nine months after the arrival of a new bull to the 15 years old cow #1542 (endocrine results of this female are shown in Fig. 2a). After this abortion, a calf was born 947 days after the arrival of the new bull, and the pairing of the two animals led to further pregnancies in the following years.

3.2. Endocrine profiles after transfers

Of the 45 female transfers listed in Table 1, hormone data were available for seven animals before and after the transfer. In three of these animals, aged 6, 19, and 23 years, there was an improvement in estrous cycle activity, and there was no change in the cycle category in two animals aged 20 and 23 years, respectively. In two transfers of female #362, estrous cycle activity worsened after transporting this animal from Salzburg to Usti nad Labem and back to Salzburg. However, during the transfers, the animal was already 26 and 27 years old. On the other hand, data were available from a 30-year-old female (#291; not included in Table 1) who was transferred from Antwerp to Thoiry at 30. In this animal, the category of the estrous cycle improved from four to two after arrival.

The hormone analysis results after a bull's transfer are included in Table 2. The cycle category before and after a transfer was determined in 26 of 83 females (31.3%). The results were 2 (2.4%), 12 (14.5%), and 12 (14.5%) in the categories 'deteriorated, neutral, positive', respectively. The other 68.6% were classified as 'unknown' because either no samples were collected, or samples were collected only before or after transfer.

Results from females #1542 and #1543 (Fig. 2) serve as an example of the hormonal analysis done in this study. They were at Copenhagen Zoo, where bull #1361 arrived in June 2012. Within two weeks of the arrival, #1542 showed signs of estrus. The first reported mating occurred in mid-September, and the second in November. As mentioned in section 4.2., rhino #1542 (Fig. 2a) had an abortion at the end of March 2013, and after two estrous cycles of approximately 70 days, she conceived and gave birth to a healthy calf in January 2015, 947 days after the males' arrival.

Rhino #1543 (Fig. 2b) was acyclic before the males' arrival but already had a luteal phase shortly before the arrival of the new bull. In the following two years, this cow was mated several times; however, none of the matings resulted in a pregnancy.

4. Discussion

This study of white rhinoceroses in European zoos analyzed the effects of animal transfers on reproductive success. The analysis was limited to sexually mature but mostly non-breeding animals transferred within the EEP. The most important success was the birth of an offspring following a transfer; for this type of evaluation, using the data included in the Studbooks for white rhinoceroses was sufficient. The hormone profiles of the female animals are supporting results for the evaluation of the effect of a transfer. Our results show that transfers resulted in births in 26.7% of female and 23.2% of male transfers; these numbers were lower than hoped.

At the turn of the millennium, several approaches were suggested to overcome the reproductive problems in the captive white rhinoceros population [10]. The cornerstones of these recommendations were hormone monitoring, transfer of animals into new breeding situations, clinical examinations of reproductive soundness, and the development of assisted reproductive techniques. Much hope was placed in the transfer of animals between zoos. About 20 years later, we see that only about 25% of females affected by transfers have given birth to offspring afterward. This is different from the expected result, but it is at least a possibility to stimulate breeding in a few animals. In addition, animal transfers are an essential factor in managing genetic variability [8,9]. To get closer to the breeding rates in the wild [2,12], two or even three additional transfers of non-breeding animals should be considered. As the past has shown, a wait-and-see position without transfers does not lead to success and very often does promote the development of reproductive tract pathologies due to asymmetric reproductive aging [19,20].

The evaluation of the results in this study focused on the transfer of adult animals aged 4–28 years. Significant findings are that in addition to the relatively low breeding success rate, sometimes a considerable amount of time elapses before a calf is born. The results of this study suggest that it is necessary to transfer relatively young females. One of the 12 transferred females who gave birth to a calf was 18 years old at the time of transfer, and the 11 other females were 15 at most. The current practice for transferring young or subadult animals in the EEP is to transfer juvenile or adolescent females out of their maternal group [6–8]. For example, under this management practice, approximately five young animals aged 2–5 years were transferred to another zoo annually between 2018 and 2022. This practice, which has been in place since 2007, is associated with an increasing birth rate in the EEP for white rhinoceroses. The number of white rhinoceroses born annually in the EEP was approximately 15 between 2014 and 2022, and the proportion of breeding female white rhinoceroses doubled from 21% to 43% between 2009 and 2017. Despite this successful doubling of breeding female white rhinoceroses in the EEP, in 2017, 49 of 96 females aged 5–20 years were classified as non-breeding [7].

Two-thirds of parturitions following female transfers (n = 12) occurred after 700–1100 days, which implies that conceptions occurred one to two years after the transfer. Two animals gave birth after 1300–1500 days, i.e., successful copulation in the third year after the transfer. Births following the arrival of a new male were more evenly distributed over five years. On the one hand, births occurred as early as 500–700 days after transfer; on the other hand, calves were born in the sixth year after the arrival of a male, although about half of the parturitions occurred within three years after a male transfer. These figures

Table 1
List of female white rhinoceros transfers.

Female studbook number	Name	Female date of birth	Date of transfer	Transfer from	Transfer to	Age at transfer (years)	Calves before transfer	Birthdate of first calf after transfer	Days between transfer and birth of a calf	Category of estrous cycle activity before transfer	Category of estrous cycle activity after transfer	Effect of transfer on estrous cycle
199	Sanny/Sanni	1966	24.08.1990	Cologne (DE)	Dvur Kralove (CZ)	24	nulliparous	-	-	no data	no data	unknown
361	Baby	1971	21.08.1991	Munich (DE)	Salzburg (AT)	20	nulliparous	-	-	4	4	neutral
362	Kathi (Mlangana)	1972	21.08.1991	Munich (DE)	Salzburg (AT)	19	nulliparous	-	-	no data	1	unknown
253	Mikume	1968	28.11.1991	Blackpool (UK)	Pelissane (FR)	23	nulliparous	-	-	no data	no data	unknown
254	Mopane	1967	28.11.1991	Blackpool (UK)	Pelissane (FR)	24	1 calf (1973)	-	-	no data	no data	unknown
258	Rosie	1969	28.11.1993	Windsor (UK)	Longleat (UK)	24	nulliparous		-	no data	no data	unknown
260	Thelma	1969	29.11.1993	Windsor (UK)	Longleat (UK)	24	nulliparous	-	-	no data	no data	unknown
261	Babs	1969	29.11.1993	Windsor (UK)	Longleat (UK)	24	nulliparous	-	-	no data	no data	unknown
262	Suki	1969	29.11.1993	Windsor (UK)	Longleat (UK)	24	nulliparous	-	-	no data	no data	unknown
931	Diuna/Dyini	1987	04.09.1997	Pretoria (ZA)	Poznan (PL)	10	nulliparous	18.11.1999	805	no data	no data	unknown
362	Kathi (Mlangana)	1972	30.06.1998	Salzburg (AT)	Usti nad Labem (CZ)	26	nulliparous	-	-	1	2 (partly 3)	deteriorated
362	Kathi (Mlangana)	1972	31.08.1999	Usti nad Labem (CZ)	Salzburg (AT)	27	nulliparous	-	-	2	4	deteriorated
773	Frederike/ Kifaru	1982	10.12.1999	Berlin TP (DE)	Salzburg (AT)	17	nulliparous	-	-	no data	4	unknown
859	Reni	1986	11.12.2000	Sofia (RO)	Dublin (IR)	14	nulliparous	-	-	no data	no data	unknown
504	Gracie	1979	01.02.2002	Paignton (UK)	Kessingland (UK)	23	nulliparous	-	-	no data	no data	unknown
651	Rohna/Gaby	1979	28.03.2003	Paris (FR)	Lisieux (FR)	24	2 calves (1987, 1992)	-	-	no data	no data	unknown
649	Kenia	1980	14.05.2003	Erfurt (DE)	Lille (FR)	23	nulliparous	-	-	3	partly 2	improved
1083	Tandamance	1993	02.09.2003	Jerusalem (IL)	Ramat Gan (IL)	10	nulliparous	23.09.2007	1482	4	-	unknown
812	Emily	1985	03.06.2004	Munster (DE)	Givskud (DK)	19	1 calf (1990)	-	-	3	partly 2	improved
643	Petra	1981	14.06.2004	Arnhem	Emmen (NL)	23	nulliparous	-	-	3	3	neutral
907	Gingabelle	1987	14.06.2004	Emmen (NL)	Arnhem (NL)	17	3 calves (1996, 1998, 1999)	-	-	no data	2 (partly 3)	unknown
1061	Zulu	1990	01.03.2007	Bewdley (UK)	Mallorca (ES)	17	nulliparous	-	-	no data	no data	unknown
964	Yvonne	1990	23.04.2009	Hilvarenbeek (NL)	Munster (DE)	19	nulliparous	-	-	no data	4 (partly 3)	unknown
1047	Makoubu	1994	24.04.2009	Whipsnade (UK)	Hilvarenbeek (NL)	15	nulliparous	02.04.2011	708	-	-	unknown
964	Yvonne	1990	12.08.2009	Munster (DE)	Hilvarenbeek (NL)	19	nulliparous	-	-	no data	no data	unknown
1009	Mirjam	1992	20.04.2010	Hilvarenbeek (NL)	Woburn (UK)	18	nulliparous	-	-	no data	no data	unknown
1501	Zola	2005	31.03.2011	Givskud (DK)	Cabarceno (ES)	6	nulliparous	26.09.2013	910	4	2	improved
1406	Iris	2002	12.09.2011	Arnhem (NL)	Tabernas (ES)	9	nulliparous	-	-	3	no data	unknown
1474	Jane	2000	05.10.2011	Blairdrummond (GB)	Munster (DE)	11	nulliparous	23.05.2013	596	no data	3	unknown
1410	Lucy	2002	21.05.2012	Bewdley (UK)	Blairdrummond (GB)	10	nulliparous	-	-	no data	no data	unknown
1596	Kara	2006	23.05.2012	Longleat (GB)	Peaugres (FR)	6	nulliparous	-	-	no data	3	unknown
1171	Namakula	1997	26.09.2012	Boras (SE)	Kolmarden (SE)	15	nulliparous	-	-	no data	no data	unknown
1463	Mafunyane	2001	13.03.2013	Montpellier (FR)	Beauval (FR)	12	nulliparous	18.11.2016	1346	no data	no data	unknown
1306	Malelane	1998	14.03.2013	Beauval (FR)	Montpellier (FR)	15	nulliparous	-	-	no data	2	unknown
1480	Izala	2004	05.11.2013	Kolmarden (SE)	Arnhem (NL)	9	nulliparous	25.01.2016	811	no data	2	unknown
1444	Manzi	2000	01.07.2014	Coulange (Amneville) (FR)	South Lakes (GB)	14	nulliparous	25.12.2016	908	3	no data	unknown
1460	Tala	1999	04.07.2014	South Lakes (GB)	Coulange (Amneville) (FR)	15	1 calf (2008)	05.03.2017	975	no data	no data	unknown
1543	Karen	2003	21.04.2015	Copenhagen (DK)	Schwerin (DE)	12	nulliparous	-	-	2	no data	unknown
1572	Mayayi	2004	02.06.2015	Valencia (ES)	Cabarceno (ES)	11	nulliparous	-	-	no data	no data	unknown
1445	Tswane	2000	27.10.2015	Coulange (Amneville) (FR)	Blairdrummond (GB)	15	nulliparous	-	-	2	no data	unknown
1410	Lucy	2002	30.10.2015	Blairdrummond (GB)	Coulange (Amneville) (FR)	13	nulliparous	-	-	no data	no data	unknown
1425	Beth	2001	12.05.2016	Kessingland (GB)	Lisieux (FR)	15	nulliparous	03.12.2018	935	no data	no data	unknown
1578	Marcita (Hildegard)	2005	12.12.2016	Osnabrück (DE)	Erfurt (DE)	11	nulliparous	29.12.2018	747	no data	2	unknown
1444	Manzi	2000	30.05.2018	South Lakes (GB)	Lisieux (FR)	18	1 calf (2008)	01.06.2021	1098	no data	3 (partly 4)	unknown
1464	Jabulani	2001	10.12.2018	Montpellier (FR)	Dvur Kralove (CZ)	17	nulliparous	-	-	no data	no data	unknown

Table 2
List of male white rhinoceros transfers. Bulls that were proven breeders before their transport are marked with a '*'. Female #1542 had an abortion before a calf was born 947 days after the new bull's arrival; the hormone profile of this female is shown in Fig. 2a. Female #767 also had an abortion before a calf was born 1724 days after the bull's arrival. Two births, 2096 and 2142 days after the arrival of a bull, are included in the table, although we have set the time limit for the calculations at five years.

Male studbook number	Male name	Male year of birth	Male arrival at new location	Male age at arrival	Transfer from	Transfer to	Female studbook number	Female name	Female year of birth	Female age at year of male transfer	Calf born after arrival of new male	Days between arrival of male and birth of calf	Category of estrous cycle activity before transfer	Category of estrous cycle activity after transfer	Effect of transfer on estrous cycle
712	George	1977	08.08.1990	13	Aalborg (DK)	Givskud (DK)	652	Sophie	1981	9	-	-	no data	no data	unknown
712	George	1977	08.08.1990	13	Aalborg (DK)	Givskud (DK)	653	Eva	1981	9	-	-	no data	no data	unknown
1013	Umkombe	1986	18.09.1991	5	Kruger NP (SA)	Lisbon (PT)	109	Turra	1967	24	-	-	no data	no data	unknown
7	Karl	1965	21.07.1993	28	Leipzig (DE)	Bandholm (DK)	231	N'Gili	1974	19	-	-	no data	no data	unknown
7	Karl	1965	21.07.1993	28	Leipzig (DE)	Bandholm (DK)	458	No name	1972	21	-	-	no data	no data	unknown
76	Balthazar*	1969	29.11.1995	26	Antwerp (BE)	Hilvarenbeek (NL)	223	Mira	1970	25	-	-	no data	no data	unknown
76	Balthazar*	1969	29.11.1995	26	Antwerp (BE)	Hilvarenbeek (NL)	835	Karlijn	1985	10	-	-	no data	no data	unknown
221	Oscar*	1968	03.10.1996	28	Hilvarenbeek (NL)	Givskud (DK)	652	Sophie	1981	15	-	-	no data	no data	unknown
221	Oscar*	1968	03.10.1996	28	Hilvarenbeek (NL)	Givskud (DK)	653	Eva	1981	15	-	-	no data	no data	unknown
828	Hannu	1983	18.04.1997	14	Knowsley (GB)	Marwell (GB)	856	Sula	1986	11	08.02.1999	661	no data	no data	unknown
828	Hannu	1983	18.04.1997	14	Knowsley (GB)	Marwell (GB)	868	Tracy	1986	11	-	-	no data	no data	unknown
828	Hannu	1983	18.04.1997	14	Knowsley (GB)	Marwell (GB)	949	Maia	1990	7	-	-	no data	no data	unknown
532	Dale	1979	20.10.1998	19	Paignton (GB)	Arnhem (NL)	230	Freya	1971	27	19.03.2002	1246	no data	2	unknown
532	Dale	1979	20.10.1998	19	Paignton (GB)	Arnhem (NL)	643	Petra	1981	17	-	-	no data	4	unknown
1025	Gilou	1992	21.06.2000	8	Lisieux (FR)	Hilvarenbeek (NL)	835	Karlijn	1985	15	-	-	no data	no data	unknown
1025	Gilou	1992	21.06.2000	8	Lisieux (FR)	Hilvarenbeek (NL)	964	Yvonne	1990	10	-	-	no data	no data	unknown
1025	Gilou	1992	21.06.2000	8	Lisieux (FR)	Hilvarenbeek (NL)	1009	Mirjam	1992	8	-	-	no data	no data	unknown
669	Niko	1981	04.12.2002	21	Liberec (CZ)	Bratislava (SK)	1154	Ada	1984	18	-	-	4	2	improved
669	Niko	1981	05.12.2002	21	Liberec (CZ)	Bratislava (SK)	1155	Sena	1984	18	-	-	4	3	improved
1165	Miguelin	1997	24.11.2004	7	Cabarceno (ES)	Hilvarenbeek (NL)	835	Karlijn	1985	19	-	-	no data	no data	unknown
1165	Miguelin	1997	24.11.2004	7	Cabarceno (ES)	Hilvarenbeek (NL)	964	Yvonne	1990	14	-	-	no data	no data	unknown
1165	Miguelin	1997	24.11.2004	7	Cabarceno (ES)	Hilvarenbeek (NL)	1009	Mirjam	1992	12	-	-	no data	no data	unknown
1552	Chaka	2000	18.12.2004	4	Kruger NP (SA)	Dublin (IR)	859	Reni	1986	18	-	-	2	no data	unknown
1048	Smoske	1994	07.06.2006	12	Arnhem (NL)	Beauval (FR)	1306	Malelane	1998	8	-	-	3	2	improved
1048	Smoske	1994	07.06.2006	12	Arnhem (NL)	Beauval (FR)	1307	Satara	1998	8	17.01.2008	589	2	no data	unknown
1233	Bhasela	1999	11.05.2007	8	Malton (GB)	Boras (SE)	1171	Namakula	1997	10	-	-	3	2	improved
1233	Bhasela	1999	11.05.2007	8	Malton (GB)	Boras (SE)	1338	Zinzi	2000	7	16.11.2011	1650	2	2	neutral
1233	Bhasela	1999	11.05.2007	8	Malton (GB)	Boras (SE)	1339	Merula	2000	7	27.01.2009	627	4	no data	unknown
1025	Gilou	1992	30.05.2007	15	Hilvarenbeek (NL)	Arnhem (NL)	907	Gingabelle	1987	20	-	-	2	Cat. 2 (3)	neutral
1025	Gilou	1992	30.05.2007	15	Hilvarenbeek (NL)	Arnhem (NL)	1340	Kwanzaa	2000	7	06.04.2010	1042	3	2	improved
1025	Gilou	1992	30.05.2007	15	Hilvarenbeek (NL)	Arnhem (NL)	1406	Iris	2002	5	-	-	no data	3	unknown
1284	Kifarou	2000	06.06.2007	7	Malton (GB)	Kessingland (GB)	1425	Beth	2001	6	-	-	no data	no data	unknown

(*continued on next page*)

Table 2 (*continued*)

Male studbook number	Male name	Male year of birth	Male arrival at new location	Male age at arrival	Transfer from	Transfer to	Female studbook number	Female name	Female year of birth	Female age at year of male transfer	Calf born after arrival of new male	Days between arrival of male and birth of calf	Category of estrous cycle activity before transfer	Category of estrous cycle activity after transfer	Effect of transfer on estrous cycle
1424	Joby	2001	28.06.2007	6	Kessingland (GB)	Montpellier (FR)	1463	Mafunyane	2000	7	-	-	3	no data	unknown
1424	Joby	2001	28.06.2007	6	Kessingland (GB)	Montpellier (FR)	1464	Jabulani	2001	6	-	-	2	no data	unknown
796	Christian	1984	19.02.2008	24	Peaugres (FR)	La Palmyre (FR)	767	Noelle	1982	26	08.11.2012	1724	3	3	neutral
1538	Yuli	1993	01.05.2009	16	Estepona (ES)	Coulange (FR)	1444	Manzi	2000	9	-	-	3	3	neutral
1538	Yuli	1993	01.05.2009	16	Estepona (ES)	Coulange (FR)	1445	Tswane	2000	9	-	-	3	3	neutral
1360	Otto	1997	26.11.2009	12	Bandholm (DK)	Colchester (GB)	1457	Emily	2000	9	13.04.2013	1234	2	2	neutral
829	Budweiser*	1985	16.06.2010	25	Knowsley (GB)	Kessingland (GB)	1425	Beth	2001	9	-	-	no data	no data	unknown
1489	Rimbo	2004	10.11.2010	6	Lille (FR)	Pelissane - La Barben (FR)	1683	Wanza	2003	7	-	-	no data	no data	unknown
1489	Rimbo	2004	10.11.2010	6	Lille (FR)	Pelissane - La Barben (FR)	1684	Bela	2003	7	-	-	no data	no data	unknown
1581	Amari	2005	25.01.2011	6	Lille (FR)	Dortmund (DE)	1659	Shakina	2005	6	21.04.2014	1182	no data	no data	unknown
1581	Amari	2005	25.01.2011	6	Lille (FR)	Dortmund (DE)	1627	Jasira	2005	6	23.09.2014	1337	no data	no data	unknown
1352	Kei/Kaj	2000	04.05.2011	11	Givskud (DK)	Woburn (GB)	1713	Mkuzi	2005	6	-	-	no data	no data	unknown
1352	Kei/Kaj	2000	04.05.2011	11	Givskud (DK)	Woburn (GB)	1714	Mtubatuba	2005	6	-	-	no data	no data	unknown
1212	Otzee	1998	25.05.2011	13	Woburn (GB)	Givskud (DK)	812	Emily	1985	26	-	-	4	2	improved
1212	Otzee	1998	25.05.2011	13	Woburn (GB)	Givskud (DK)	1251	Inger/Enkeli	1999	12	-	-	2	2	neutral
2075	Benny	2004	02.02.2012	8	Thaba Man (SA)	Coulange (FR)	1444	Manzi	2000	12	-	-	4	2 (3)	improved
2075	Benny	2004	02.02.2012	8	Thaba Man (SA)	Coulange (FR)	1445	Tswane	2000	12	-	-	3	2	improved
2075	Benny	2004	02.02.2012	8	Thaba Man (SA)	Coulange (FR)	2073	Yoruba	2007	5	02.07.2016	1612	3	2	neutral
2075	Benny	2004	02.02.2012	8	Thaba Man (SA)	Coulange (FR)	2074	Hekaw	2004	8	01.12.2014	1033	3	3	neutral
1540	Curt	1997	12.06.2012	15	Copenhagen (DK)	Nyíregyháza (HU)	1556	Sakile	2001	11	12.10.2016	1583	4	2	improved
1361	Oscar	1996	21.06.2012	16	Bandholm (DK)	Copenhagen (DK)	1543	Karen	1997	15	-	-	4	2	improved
1361	Oscar	1996	21.06.2012	16	Bandholm (DK)	Copenhagen (DK)	1542	Minna	1997	15	24.01.2015	947	4	2	improved
1466	Shaka	2003	10.12.2012	9	Malton (GB)	Bandholm (DK)	1362	Berta	1998	14	-	-	no data	no data	unknown
1466	Shaka	2003	10.12.2012	9	Malton (GB)	Bandholm (DK)	1363	Bodil	1997	15	-	-	no data	no data	unknown
1526	Bantu	2005	29.04.2014	9	Kerkrade (NL)	Augsburg (DE)	1625	Chris	2005	9	18.02.2016	660	3	2	improved
1526	Bantu	2005	29.04.2014	9	Kerkrade (NL)	Augsburg (DE)	1626	Kibibi	2005	9	06.02.2016	648	2	2	neutral
1525	Rafika	2005	20.05.2014	9	Kerkrade (NL)	Veszprem (HU)	1280	Rebeca	2000	14	14.2.2020	2096	2	no data	unknown
1525	Rafika	2005	20.05.2014	9	Kerkrade (NL)	Veszprem (HU)	1691	Naruna	2008	6	-	-	3	no data	unknown
1165	Miguelin	1997	28.05.2014	17	Hilvarenbeek (NL)	Kerkrade (NL)	1447	Frieda/Lia	2002	12	-	-	no data	no data	unknown
1393	Limpopo	2001	22.04.2015	14	Schwerin (DE)	Hilvarenbeek (NL)	964	Yvonne	1990	25	-	-	no data	no data	unknown
1393	Limpopo	2001	22.04.2015	14	Schwerin (DE)	Hilvarenbeek (NL)	1047	Makoubu	1994	21	-	-	no data	no data	unknown

(*continued on next page*)

Table 2 (*continued*)

Male studbook number	Male name	Male year of birth	Male arrival at new location	Male age at arrival	Transfer from	Transfer to	Female studbook number	Female name	Female year of birth	Female age at year of male transfer	Calf born after arrival of new male	Days between arrival of male and birth of calf	Category of estrous cycle activity before transfer	Category of estrous cycle activity after transfer	Effect of transfer on estrous cycle
1165	Miguelin*	1997	21.05.2015	18	Kerkrade (NL)	Osnabruck (DE)	1578	Marcita	2005	10	-	-	no data	2	unknown
1165	Miguelin*	1997	21.05.2015	18	Kerkrade (NL)	Osnabruck (DE)	1628	Amelie	2007	8	-	-	no data	no data	unknown
2102	Pamir	2008	19.11.2015	7	Cambron (BE)	Dvur Kralove (CZ)	1043	Bata/ Jessica	1994	11	-	-	no data	no data	unknown
1652	Kimba	2008	27.09.2016	8	Lille (FR)	Schwerin (DE)	1687	Clara	2006	10	-	-	2	2	neutral
1645	Flannery/ Gen	2008	27.09.2016	8	Lille (FR)	Emmen (NL)	2004	Zahra	2009	7	-	-	no data	no data	unknown
1574	Lekuruh	2004	18.10.2016	12	Gelsenkirchen (DE)	Pelissane - La Barben (FR)	1683	Wanza	2003	13	-	-	3	4	deteriorated
1574	Lekuruh	2004	18.10.2016	12	Gelsenkirchen (DE)	Pelissane - La Barben (FR)	1684	Bela	2003	13	30.08.2022	2142	2	4	deteriorated
1489	Rimbo	2004	20.10.2016	12	Pelissane - La Barben (FR)	Gelsenkirchen (DE)	1575	Tamu	2004	12	-	-	no data	no data	unknown
1489	Rimbo	2004	20.10.2016	12	Pelissane - La Barben (FR)	Gelsenkirchen (DE)	1576	Cera	2004	12	-	-	no data	no data	unknown
1360	Otto*	1997	02.11.2016	19	Colchester (GB)	Woburn (GB)	1713	Mkuzi	2005	11	-	-	no data	no data	unknown
1360	Otto*	1997	02.11.2016	19	Colchester (GB)	Woburn (GB)	1714	Mtubatuba	2005	11	-	-	no data	no data	unknown
1526	Bantu*	2005	22.02.2017	12	Pairi Daiza (BE)	Augsburg (DE)	1626	Kibibi	2005	12	07.10.2021	1688	2	2	neutral
1424	Joby	2001	15.03.2017	16	Montpellier (FR)	Pairi Daiza (BE)	2101	Madiba	2008	9	25.11.2019	985	no data	no data	unknown
2039	Troy/Balu	2010	27.04.2017	7	Malton (GB)	Montpellier (FR)	1306	Malelane	1998	19	-	-	2	no data	unknown
2039	Troy/Balu	2010	27.04.2017	7	Malton (GB)	Montpellier (FR)	1464	Jabulani	2001	16	-	-	2	no data	unknown
1648	L.Pancho	2008	09.03.2018	10	Emmen (NL)	Valbremo - Le Cornelle (IT)	2021	Geraldine	2009	8	-	-	no data	no data	unknown
1648	L.Pancho	2008	09.03.2018	10	Emmen (NL)	Valbremo - Le Cornelle (IT)	2081	Lara	2011	7	-	-	no data	no data	unknown
1360	Otto*	1997	25.06.2018	21	Woburn (GB)	Colchester (GB)	2150	Astrid	2013	5	14.10.2020	842	no data	no data	unknown
1709	Pembe	2009	15.12.2018	9	Estepona (ES)	Knowsley (GB)	1584	Binta	2005	13	-	-	no data	no data	unknown
1709	Pembe	2009	15.12.2018	9	Estepona (ES)	Knowsley (GB)	2041	Jaseera	2011	7	-	-	no data	no data	unknown

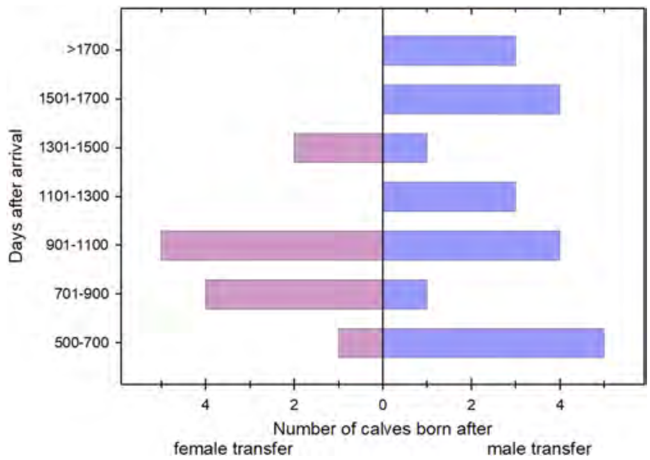

Fig. 1. Illustration of the number of days between the transfer of a female or the arrival of a new bull and a resulting birth.

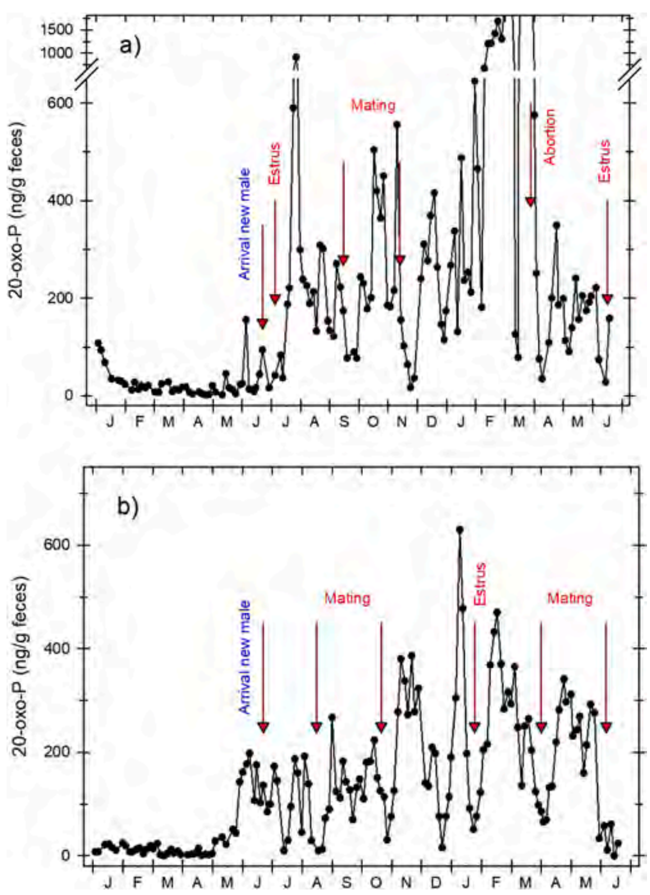

Fig. 2. Hormone profiles of rhinoceros females #1542 (a) and #1543 (b) during periods before and after a new male was introduced.

show that it can take some time before a successful mating between new partners occurs and that it is worth having some patience after transfers.

The results of endocrine analysis, especially after the transfer of a bull, are promising; however, hormone data could only be analyzed from 26 females before and after the arrival of a new bull. Thirteen of the 26 animals showed an improvement in the cycle category. If category two is considered the most promising for reproduction, it was present in 19 females after the transfer of a bull. However, the cycle category before pregnancy is not the sole determining characteristic for fertilization. A recent study analyzed preconception endocrine profiles in the white rhinoceros. Conceptions occurred after all types of estrous cycles, i.e., cycles of about 15, 35, and 70 days, and even after periods of ovarian inactivity [18].

The success rates of transfers are relatively modest, and it is unclear why pregnancy does not occur more frequently after a transfer. Acyclicity and the generally low reproductive success of ex-situ white rhino populations need further research. In addition, the effects of a new bull are highly individualized. For example, the transfer of bull #1574 (Lekuruh) to the "Parc Zoologique de La Barben" stopped the cycle of the resident female rhino #1684 (Bela), which subsequently became acyclic. Due to this acyclicity, endocrine monitoring was terminated after two years, and further development until the conception of cow #1574 is unknown. Nevertheless, a calf was born from this pairing 2142 days, the sixth year, after the arrival of the new bull.

The transfer of southern white rhinoceroses between different zoos is insufficient to solve the reproductive difficulties of rhinoceroses in captivity. An additional tool would be artificial insemination following ovulation induction. Semen collection and the use of frozen-thawed ejaculates for artificial insemination in white rhinoceroses have been established; however, the success rate of AI procedures in this species is only modest [30–32].

This study could not fully answer why females do not breed after transfers even if there was a positive hormonal effect, as it is limited to Studbook and hormone data only. Effects of, e.g., herd management, social environment, or enclosure size could not be considered. Creating conditions for species-typical social and reproductive behavior is difficult to ensure in zoos [8,9]. Rhinoceroses may show spatial distress and hierarchical repression of conception when insufficient space exists [2, 14–16,27]. Another obstacle in captive rhinoceros management is feeding, which is suspected to affect fertility. Supplementary feeding, for example, increased the conception rates in game-ranched rhinoceroses in South Africa [33]. However, the white rhinoceroses in the EEP are more likely to be overweight than normal and certainly are not underweight. Phytoestrogens, present, e.g., in clover hay or soy and alfalfa-based pellets, may have adverse effects on the reproductive health of white rhinoceroses [34], although the use of feeds containing phytoestrogens does not seem to be very widespread in the EEP.

4.1. Conclusion

During the past decades, the fertility of white rhinoceroses kept in zoos has been low, and female rhinoceroses that never bred are at a particularly increased risk of developing reproductive tract pathologies [19,20]. One management measure to stimulate breeding is to transfer non-reproducing animals to other zoos [11]. The transfers examined in this study resulted in parturitions in a quarter of the cases, with conceptions taking place a few months to up to five, and in exceptional cases, even six years after a transfer. Endocrine data before and after a male transfer were determined in about 30% of females affected by a male transfer. A positive development of estrous cycle activity after the arrival of the new bull occurred in half of these females. This study's relatively low success of transfers relates to the partly advanced age of the white rhinoceroses studied. A higher success rate can be achieved by transferring juvenile or adolescent animals. Therefore, the European breeding program for white rhinoceroses recommends transferring young females from their maternal group into a new herd. By implementing this practice, the number of calves born annually and the proportion of breeding female white rhinoceroses in the total population has increased significantly in recent years [6–8].

CRediT authorship contribution statement

Franz Schwarzenberger: Conceptualization, Methodology, Project administration, Writing – review & editing, Supervision. **Caroline Pannrucker**: Methodology, Data curation, Formal analysis, Writing –

original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the veterinarians, animal keepers, and curators of the many zoos that have worked with us over the decades. We particularly thank the studbook keeper for the European white rhinoceros breeding program, Lars Versteege, Hilvarenbeek (NL), for sharing information on white rhinoceros transfers in Europe. The hormone analyses were billed to the zoos according to the number of samples analyzed. Between 2000 and 2005, this work received support from a grant from the 'Joint IRF/SOS Rhino research program 1999′ (IRF International Rhino Foundation).

References

[1] M.H. Knight, African Rhino specialist group chair report - Rapport du Groupe de Spécialistes du Rhinocéros d′Afrique. Pachyderm 63 (2021) 17–32.
[2] P. Kretzschmar, H. Auld, P. Boag, U. Gansloßer, C. Scott, P.J. van Coeverden de Groot, et al., Mate choice, reproductive success and inbreeding in white rhinoceros: new insights for conservation management, Evolut. Appl. 13 (4) (2020) 699–714, https://doi.org/10.1111/eva.12894.
[3] H.S. Clements, D. Balfour, E. Di Minin, Importance of private and communal lands to sustainable conservation of Africa's rhinoceroses, Front. Ecol. Environ. (2023), https://doi.org/10.1002/fee.2593.
[4] IUCN. The IUCN Red List of Threatened Species. https://www.iucnredlist.org/search?query=Rhinoceroses&searchType=species [accessed 30. 3.2023].
[5] Ogden J. International Studbook for the White Rhinoceros Volume 12 (Ceratotherium simum). Bay Lake FL, USA, 2011.
[6] Versteege L. European Studbook White Rhino, 2014 [Ceratotherium simum], 4th ed. Beekse Bergen, Hilvarenbeek, The Netherlands, 2015.
[7] Versteege L. European Studbook White Rhino, 2017 [Ceratotherium simum], 5th ed. Beekse Bergen, Hilvarenbeek, The Netherlands, 2018.
[8] Versteege L. EAZA White rhino EEP Best Practice Guidelines. Beekse Bergen, Hilvarenbeek, The Netherlands, 2018.
[9] T.J. Foose, R.J. Wiese, Population management of rhinoceros in captivity, Int. Zoo. Yb. 40 (1) (2006) 174–196, https://doi.org/10.1111/j.1748-1090.2006.00174.x.
[10] F. Schwarzenberger, C. Walzer, S. Silinski, K. Tomasova, F. Göritz, T. Hildebrandt, R. Hermes, Problems associated with the low reproductive rate in captive white rhinoceroses (Ceratotherium simum) an update, Verh. Ber. Erkrg. Zootiere 41 (2003) 301–303.
[11] C.E. Reid, L. Versteege, A. Ludwig, R. Hermes, Analysis of the European captive Southern white rhinoceros Ceratotherium simum simum population using the International Studbook for the African White Rhinoceros (2001-2004) and integrating reproductive health findings, Int. Zoo. Yb. 46 (1) (2012) 209–220, https://doi.org/10.1111/j.1748-1090.2011.00164.x.
[12] Owen-Smith RN, Megaherbivores: the influence of very large body size on ecology. Cambridge studies in ecology, Cambridge Univ. Press,, 1992.
[13] Scott, S.E. Cain, B. Kort, S.R. de, B. Johnson, C. Khayale, L. Versteege, et al., Group composition impacts reproductive output and population viability in captive white rhinoceros, Anim. Conserv. (2022), https://doi.org/10.1111/acv.12833.
[14] I. Cinková, A.M. Shrader, Individuality, species-specific features, and female discrimination of male southern white rhinoceros courtship calls, Anim. Cogn. 25 (4) (2022) 769–782, https://doi.org/10.1007/s10071-021-01591-4.
[15] M. Hutchins, M.D. Kreger, Rhinoceros behaviour: Implications for captive management and conservation, Int. Zoo. Yb. 40 (1) (2006) 150–173, https://doi.org/10.1111/j.1748-1090.2006.00150.x.
[16] L.C. Metrione, L.M. Penfold, G.H. Waring, Social and spatial relationships in captive southern white rhinoceros (Ceratotherium simum simum), Zoo. Biol. 26 (6) (2007) 487–502, https://doi.org/10.1002/zoo.20143.
[17] K. Radeke-Auer, A. Wittwer, J. Aust, M. Roller, D.W.H. Müller, F. von Houwald, et al., Reproductive non-seasonality in rhinoceroses: a review of the in-situ literature and birth records of ex-situ institutions, 23-30-30, J. Zoo. Aquar. Res. 10 (1) (2022), https://doi.org/10.19227/jzar.v10i1.628.
[18] F. Schwarzenberger, R. Hermes, Comparative analysis of gestation in three rhinoceros species (Diceros bicornis; Ceratotherium simum; Rhinoceros unicornis), Gen. Comp. Endocrinol. 334 (2023), 114214, https://doi.org/10.1016/j.ygcen.2023.114214.
[19] R. Hermes, T.B. Hildebrandt, F. Göritz, Reproductive problems directly attributable to long-term captivity - asymmetric reproductive aging, Anim. Reprod. Sci. 82–83 (2004) 49–60, https://doi.org/10.1016/j.anireprosci.2004.05.015.
[20] R. Hermes, T.B. Hildebrandt, C. Walzer, F. Göritz, M.L. Patton, S. Silinski, et al., The effect of long non-reproductive periods on the genital health in captive female white rhinoceroses (Ceratotherium simum simum, C.s. cottoni), Theriogenology 65 (8) (2006) 1492–1515, https://doi.org/10.1016/j.theriogenology.2005.09.002.
[21] R. Hermes, T.B. Hildebrandt, S. Blottner, C. Walzer, S. Silinski, M.L. Patton, et al., Reproductive soundness of captive southern and northern white rhinoceroses (Ceratotherium simum simum, C.s. cottoni): Evaluation of male genital tract morphology and semen quality before and after cryopreservation, Theriogenology 63 (1) (2005) 219–238, https://doi.org/10.1016/j.theriogenology.2004.04.007.
[22] F. Schwarzenberger, C. Walzer, K. Tomasova, J. Vahala, J. Meister, K.L. Goodrowe, et al., Faecal progesterone metabolite analysis for non-invasive monitoring of reproductive function in the white rhinoceros (Ceratotherium simum), Anim. Reprod. Sci. 53 (1–4) (1998) 173–190, https://doi.org/10.1016/S0378-4320(98)00112-2.
[23] M.L. Patton, R.R. Swaisgood, N.M. Czekala, A.M. White, G.A. Fetter, J. P. Montagne, et al., Reproductive cycle length and pregnancy in the Southern White Rhinoceros (Ceratotherium simum simum) as determined by fecal pregnane analysis and observations of mating behavior, Zoo. Biol. 18 (2) (1999) 111–127, https://doi.org/10.1002/(SICI)1098-2361(1999)18:2<111::AID-ZOO3>3.0.CO;2-0.
[24] F. Schwarzenberger, J.L. Brown, Hormone monitoring: an important tool for the breeding management of wildlife species. Wiener Tierärztliche Monatsschrift, Vet. Med. Austria 100 (2013) 209–225.
[25] T.L. Roth, A review of the reproductive physiology of rhinoceros species in captivity, Int. Zoo. Yb. 40 (1) (2006) 130–143, https://doi.org/10.1111/j.1748-1090.2006.00130.x.
[26] F. Schwarzenberger, E. Möstl, R. Palme, E. Bamberg, Faecal steroid analysis for non-invasive monitoring of reproductive status in farm, wild and zoo animals, Anim. Reprod. Sci. 42 (1–4) (1996) 515–526, https://doi.org/10.1016/0378-4320(96)01561-8.
[27] J. Jenikejew, J. Wauters, M. Dehnhard, M. Scheumann, Linking socio-sexual and vocal behaviour with faecal progesterone and oestrogen metabolite levels in Southern white rhinoceros females, Conserv. Physiol. 9 (1) (2021) coab098, https://doi.org/10.1093/conphys/coab098.
[28] Rhinos of the World. https://www.worldrhino.com/europe/ [Accessed 30 March 2023].
[29] Belik, J. Rhinos in Europe. https://www.worldrhino.com/white-rhinos-european-zoo [Accessed 30 March 2023].
[30] R. Hermes, F. Göritz, J. Saragusty, E. Sós, V. Molnar, C.E. Reid, et al., First successful artificial insemination with frozen-thawed semen in rhinoceros, Theriogenology 71 (3) (2009) 393–399, https://doi.org/10.1016/j.theriogenology.2008.10.008.
[31] T.B. Hildebrandt, R. Hermes, C. Walzer, E. Sós, V. Molnar, L. Mezösi, et al., Artificial insemination in the anoestrous and the postpartum white rhinoceros using GnRH analogue to induce ovulation, Theriogenology 67 (9) (2007) 1473–1484, https://doi.org/10.1016/j.theriogenology.2007.03.005.
[32] P.M. Pennington, B.S. Durrant, Assisted reproductive technologies in captive rhinoceroses, Mam. Rev. 49 (1) (2019) 1–15, https://doi.org/10.1111/mam.12138.
[33] C. Ververs, M. van Zijll Langhout, M. Hostens, M. Otto, J. Govaere, B. Durrant, et al., Reproductive performance parameters in a large population of game-ranched white rhinoceroses (Ceratotherium simum simum), PLoS ONE 12 (12) (2017), e0187751, https://doi.org/10.1371/journal.pone.0187751.
[34] C.W. Tubbs, White rhino diet-induced infertility, in: E.R. Miller, N. Lamberski, P. P. Calle (Eds.), Fowler's Zoo and Wild Animal Medicine - Current Therapy, volume 10, Elsevier, St. Louis, MO, USA, 2023, pp. 621–626.