

White rhino ecology, a comparison of two rhino populations (*Ceratotherium simum simum*) in South Africa and Uganda

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Introduction

In the early 1970s, the now Professor Norman Owen-Smith of the University of Witwatersrand, South Africa, conducted research on the behavioural ecology of white rhinos over a three-and-a-half-year period, in the Hluhluwe-iMfolozi area, South Africa, for his PhD thesis presented in 1973.

Rhino Fund Uganda (RFU) collected white rhino behaviour data at the Ziwa Rhino Sanctuary (RS), Uganda, for some 10 years which have been published in a series of papers and reports updated in 2021 (Patton and Genade 2021).

This paper examines similarities and differences in the results and conclusions made on aspects of white rhino (*Ceratotherium simum simum*) behaviour between the studies. It is of importance to managers, since the earlier work was carried out in an extensive area with a long-established population, while the latter was in a smaller enclosed area with an introduced, low-density population, more akin to many white rhino conservation areas today. The smaller size landscape available to rhinos is increasingly becoming the norm in conservation settings today, as rhino populations are secured in intensive protection zones (IPZs).

Hluhluwe-iMfolozi has a sub-tropical climate with temperatures ranging from 11°C in May to 24°C in August. From December to February, mean temperatures increase to 29°C, but can be higher. The rainfall patterns in the study years in Hluhluwe-iMfolozi were characterized by summer droughts and late rains. The driest conditions prevailed in January 1970. The total annual rainfall of 1,545 mm, in 2022 represented an average year.

In Ziwa RS, Nakasongola district in central

Uganda during the study period 2017–2019, 31°C was the average maximum temperature. The wet season occurs from March to November, with a dry period in June and July. There is little rain during the dry season (December to February).

The variation in climate may have a bearing on the differences observed in this comparative study.

Use of Space

Owen-Smith reported that territorial male rhinos occupied mutually exclusive home ranges of 0.7 to 2.6 km² that were co-habitated by 0 to 3 subordinate adult males. He concluded that the ranges were defended by males and therefore should be considered territories.

The male territories of the RFU studies at the ZRS developed from three mutually exclusive areas to three areas with one male sharing part of its territory with another male and limited overlap of all three territories. The core areas within the territories showed almost complete exclusivity of one male, with the other two sharing much of the cores. The three male territories of ZRS were 5.7 km², 11.1 km² and 23.3 km² respectively, with core areas of 1.7 km², 2.01 km² and 4.2 km².

The male with the noticeably large territory was very aggressive towards the other two males, who avoided contact with him as much as possible. These two males shared part of their territory, but both were responsible for breeding. They were accepting of each other, sometimes seen as close as 30 metres. Both fought the solitary male when they came into contact, so neither was a subordinate.

Owen-Smith reported that ranges covered between 10 km² and 15 km² which included corridors but with movements restricted to the core areas of 6 km² to 8 km² during optimal grazing conditions. The actual data given were:

The mean home range was 11.6 km² (range 8.9–14.7); core area was 6.7 km² (range 5.3–9.6)

The mean home range of ZRS was 16.2 km² (range 5.6–41.6); core area was 2.4 km² (range 1.1–5.4)

A female (in the RFU study) moved long distances (considered to be due to male avoidance), while another changed its range during the year. If the data for these two are removed, the mean home range reduces to 9.8 km² and core area to 1.5 km². The water points were abundant in ZRS and replenished in dry periods.

Owen-Smith stated that individual females each had a preferred area of occupancy which was different from that of other individuals, though there was extensive, multiple overlapping between the two various ranges.

The ZRS core area map for RFU females (Fig. 1) shows overlaps of 2, 3, 4 and 7 individuals sharing the same cores, suggesting that there was more sharing of preferred areas than found by Owen-Smith.

Activity¹

The basic daily activity schedule reported by Owen-Smith was confirmed by the RFU data.

Both found no striking differences between the activity patterns exhibited by adult males, adult females, and subadults.

Owen-Smith found that over a 24-hour period, rhinos of all age/sex classes devoted 12 hours to feeding, 8.5 hours to resting and the remaining 3.5 hours to mixed activities (walking, standing alert, wallowing, and social interactions).

¹Major categories of behaviours (activities) as described by Kendal (2018):

- i. Grazing: foraging on the food plant or parts of available food.
- ii. Moving: traveling to different feeding ground while performing other social behaviours.
- iii. Resting: this is the activity without movement that includes standing, sitting, lying, sleeping.
- iv. Wallowing: animals remain submerged in water for thermo-regulatory activity.
- v. Other Activities: playing, aggression, sexuality, sympatric behaviour, territorial encounters, etc.

The RFU data, as shown by the 24-hour clock, contain a significant amount of detailed night time. Data are similar to that of Owen-Smith, which show rhinos spending some 50% of their time feeding (12 hours), 33% resting (8 hours), and 17% moving/mixed activities (4 hours).

However, much of the moving involved feeding at the same time. This meant that rhinos could be taken to the ground spend up to 16 hours a day feeding, 6 hours resting, and 2 hours moving/mixed activities.

Grazing

Owen-Smith reported that white rhinos were entirely grazers that preferred short grass but used tall grass during late dry periods. At least 30 different grass species were recorded on the terrain. However, 12 species comprised about 95% of the food intake.

Forbs made up only about 1% of the food intake and in most cases seemed to be eaten accidentally when mixed with grasses.

The RFU study found that of the 23 recorded species, rhinos grazed 14 species while 9 of them were not grazed. Forbs also made up only a small proportion of the diet, but two were preferentially grazed rather than accidentally grazed.

Both Owen-Smith and the RFU monitors noted a particular preference for grazing the grass found on termite mounds.

Drinking

Owen-Smith reported that, when pools were plentifully scattered, rhinos paused to drink sometimes twice a day and or at any time. During the late dry periods, drinking took place every 2–3 days as water supplies became restricted and the rhinos were forced to undertake a special journey to one of the remaining water holes. Visits to the water holes usually began in the late afternoon.

Sixty per cent of the rhinos drank water between 1700 and 2100 hours, another 26% thereafter, and only 14% drank during daylight hours. After a hot day, peak numbers of rhinos were not recorded until 2000 to 2100 hours.

The RFU monitors found that the main drinking period was between 1500 and 1800 hours (44%) in all weather conditions. Depending on the weather, especially during dry periods, there was also some extension to the main period where there was limited drinking from 1400 to 1500 (6%), 1800 to 2100 (19%) and 0900 to 1100 (8%) hours.

The number of times a rhino would drink per day was 0 to 3 times. About 30% of ZRS was marshland, and rhinos were often found feeding on short, soft grass that was fully or partially exposed as the swamp retreated in drier periods. It was clear that while grazing the rhinos could take in water directly or from the high moisture content of waterlogged grass.

Reproduction

Owen-Smith reported that persistent companionship of a female by a male rhino over a period of up to 20 days was a reliable indication that the female was entering or in oestrus. Territorial bulls confined pre-oestrus females for between 4 and 20 days prior to mating. These consort relationships ended between 2 and 6 days after copulation.

Owen-Smith observed seven copulations that lasted between 15 and 28 minutes. All were seen at various times during the day, but Owen-Smith concluded that there was no reason why mating should not occur at night. As only in one case a repeat mating was observed (after 3 hours), it seemed that a single copulation was the norm, leading to the conclusion that oestrous is apparently terminated by a successful copulation and consequently lasts about one day.

Oestrus data are confirmed by those of RFU research, which showed a pre-oestrus period of between 1 and 24 days and a post-copulation period of 1 to 8 days for 24 encounters.

Owen-Smith found that the first oestrus occurred at about 5 years of age, while the RFU calving data show that it occurred much earlier. The mean age at first calving for six females was 5 years 2 months and 18 days, which, based on a 16-month gestation period (see below), gives a conception mean of 3 years 10 months and 12 days. The earliest conception was at 3 years, 1 month and 20 days.

Furthermore, Owen-Smith reported that females came into oestrus when the calf was 6–12 months old. However, three of the ZRS females mated when their calves were 2, 4 and 5 months old, respectively. The average interval between their first and second calves for the first six calving females mentioned above, was estimated to be 34 months.

The early age at first calving recorded (5 years

2 months and 18 days) followed by the extended inter calving interval (34 months) suggests that it is not the onset of returning oestrus that dictates when the females will mate, but whether they have reached a level of fitness naturally required to support a new calf.

Owen-Smith found that two peaks in oestrus levels occurred in November and February resulting in peak calving months in March and July, the main calving months being March to May, but, with variability in rainfall patterns, calves were born year-round, and in any month.

Of the three calvings at the ZRS, 17 occurred in three months (June (7), August (5), January (5)) and there were no births in May or November.

RFU monitors recorded a much greater number of copulations, which showed that while most occurred only once per day, they could be repeated two, three, or four times in one day. The copulations lasted on average 17 minutes (range 5–50, n=83).

A total of 71% of the copulations occurred during the day and 29% during the night. On 14 occasions, where copulations occurred more than once on the same day, there was an average of 4 hours between each (range 1–9 hours).

Owen-Smith found that the male usually remained with the female for 2 to 6 days after copulation, which was confirmed by the RFU data of 0 to 8 days.

Gestation period data were also similar with nine records from Owen-Smith's studies suggesting probably 16 months (around 487 days), while RFU data estimated a mean of 26 gestation periods of 493 days (range 484–502)

Owen-Smith considered the age at first calving to be 6.5 to 7 years, and this is widely used in the literature. However, the RFU data showed that the first six recorded calvings averaged 5 years 2 months and 18 days. The ease of opportunity and the aggressive nature of the male probably led to particularly early mating, but it is clear that the female is capable of reproducing around a year earlier than is usually referenced.

Parturition was not observed by Owen-Smith while RFU monitors observed and recorded rhino births, one of which was analysed for a research paper (Patton and Genade 2015).

Owen-Smith observed that the previous calf or other companions were driven away or avoided only a day or less before the birth and normally did not rejoin the mother again, but had few observations to indicate

how the longstanding and close bond was broken.

However, RFU monitors recorded nine occasions of the time from when the former calf was chased and the birth of the new calf with an average of 6 hours 8 minutes (range 2 hours 17 minutes to 16 hours 59 minutes). On 14 occasions, the former calf stayed up to 50 metres from the new calf for between 3 and 57 hours. On three occasions, the former calf stayed with the new calf and formed an association.

The action of chasing started only a few hours before the birth and varied from highly aggressive to passive, but in all cases the current calf quickly worked their way back or remained within 50 metres while occasionally the female did not even bother to chase the calf off at all.

Owen-Smith observed that calves under two months of age nursed frequently and those between two and 12 months nursed about half as much. Nursing continued until calves were well over a year in most cases, but the frequency declined after 15–18 months. There were three records of nursing by calves over 18 months of age, in one instance by a 24-month-old calf.

RFU recorded some aspects of suckling from January 2017 to the end of May 2019 for eight females with new calves. During the period, some 4,178 suckling observations were made.

The average number of sucklings per day for each of the eight females was 3 (range 2 to 4) and the range in number of sucklings per day across all records was 1 to 12.

The 4,178 suckling records could be apportioned by the age of the calf, in months:

0–6m 35%; 7–12m 22%; 13–18m 23%;
19–24m 14%; and 25+m 5%

The reduction in the amount of suckling as the calf gets older would be expected as it gradually weans off milk to feeding on grass (grazing) and drinking water.

The average ICI estimated by Owen-Smith was 30 months with a range of 22 to 36 months.

In RFU research, the average inter calving interval for 25 records was 25 months with a range of 18 to 36 months. It appears that, with better grazing conditions, females recover their body condition faster and will reproduce again sooner.

Social

According to Owen-Smith, young males were considered adult at 10–12 years of age, some becoming solitary at 8 years of age. Two young males at ZRS split up after a fight when one was 7 years and 10 months old and the other 7 years and 5 months old. The younger, large for his age and very aggressive, became a breeding male at 8 years and 7 months, while the older remained solitary.

Adult females were usually accompanied by a single offspring, or a "surrogate" bond was formed with a single adolescent, which may have been a former calf but unlikely, or up to six adolescents.

Following 22 calvings, the RFU monitors recorded only three adolescents who remained with their mother and new calf, four joined one particular female and her calf, with fifteen joining sub-adult groups of between two and five individuals.

Owen-Smith reported that, although groups may be isolated from other groups, sometimes several groups may be found feeding in the same vicinity. The two main RFU subadult groups joined to form a settled group of nine.

Discussion

In general, the RFU data collected over 10 years support the observations and some speculations made by Owen-Smith. An important difference between the research is that in the smaller and wetter areas of ZRS the onset of oestrus is three years; in Hluhwe-iMfolozi it was five years leading to earlier first calvings. In addition, the average inter calving interval is typically 24 months, not 30 months.

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1 Chair reports/Rapports des Présidents

- 1 African Elephant Specialist Group Chair report/ Rapport du Groupe de Spécialistes de l'Eléphant d'Afrique

Benson Okita-Ouma and Rob Slotow

- 13 African Rhino Specialist Group Chair report/ Rapport du Groupe de Spécialistes du Rhinocéros d'Afrique

Mike Knight, Keit Mosweu, Sam M Ferreira

- 31 Asian Rhino Specialist Group Chair report/ Rapport du Groupe de Spécialistes du Rhinocéros d'Asie

Bibhab K Talukdar

37 Research

- 37 A culture of aggression: the Gorongosa elephants' enduring legacy of war

Joyce Poole, Jason Denlinger, Dominique Gonçalves, Petter Granli

Cover caption: A greater one-horned rhino wallowing in Kaziranga National Park, March 2022.

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63 Management

- 63 All aboard the 'Elephant Express', a practical solution for human-elephant coexistence

Anna Songhurst, Makata Baitse, Jennifer S Lalley, Sarah Lupton, Maipelo Molatlhegi, Ohitseng Mosupi, Ipelefatso Nkalolang, Botshelo Sensinyi, Amanda Stronza, Tracey L Taylor, Kurt Holle, Graham McCulloch

- 78 Twisting collars on male elephants in shrub terrain: animal welfare considerations for researchers, managers and manufacturers

Brooke Friswold, Brett Mitchell, George Gale, Antoinette Van de Water

- 92 Behaviour and habitat preferences of translocated rhinos (*Rhinoceros unicornis*) at Manas National Park, Assam, India

Deba Kumar Dutta

107 Field notes

- 107 Bridging the Rift: demonstrating large mammal landscape connectivity from Amboseli National Park to the greater Maasai Mara

Vicki Fishlock, Lydia Tiller, Norah Njiraini, Catherine Sayialel, Phyllis Lee, Cynthia Moss, Joseph Mukeka, Shadrack Ngene, Patrick Omondi

- 112 A possible case of congenital tusklessness in a male African elephant (*Loxodonta africana*)

Giacomo D'Ammando, David Daballen, David Lolchuragi, David Letityia, George Wittemyer, Vincent Obanda, Iain Douglas-Hamilton, Christopher Thouless

- 120 Integrating local and scientific ecological knowledge to assess African forest elephant (*Loxodonta cyclotis*) populations in a data-deficient region, eastern Democratic Republic of Congo

Leonard K Mubalama and Gedeon T Banswe

- 130 Speculating on transverse grooves in African elephant tusks

Ian SC Parker, Erwan Theleste, Gerhard Steenkamp

- 134 One year after the rollout of the *Coexistence Toolbox* for reducing human-elephant conflict
Tanya Onserio and Lucy King
- 140 Promoting positive interactions with the traumatised elephants of Gorongosa National Park
Joyce Poole, Jason Denlinger, Dominique Gonçalves, Test Malunga, Petter Granli
- 144 White rhino ecology: a comparison of two rhino populations (*Ceratotherium simum simum*), in South Africa and Uganda
Felix J Patton, Petra E Campbell, Angie Genade
- 149 Observations on the first inter calving interval for six, particularly early breeding white rhinos at Ziwa Rhino Sanctuary, Uganda
Felix J Patton, Petra E Campbell, Angie Genade
- 152 Book reviews**
- 152 How to raise a rhino: a biography of Anna Merz, founder of Lewa Downs black rhino sanctuary
Michael Dyer
- 153 Obituaries**
- 153 Mark and Peter Jenkins tribute by *Bongo Woodley*
- 156 Rudi van Aarde tribute by *Jason Bell*
- 158 Guidelines for contributors**

Pachyderm

October 2022—September 2023

No. 64

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African Rhino and
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