Reproductive behavior of white rhinoceros in the wild in Umfolozi Game Reserve, South Africa

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Introduction

This review is based on observations of the behavior of white rhinos made between 1966 and 1971 in the Umfolozi Game Reserve, KwaZulu-Natal, South Africa. This population existed at a high density of 3-5 animals per km^2 at that time. All adult rhinos and some sub-adults were individually identifiable from variations in horn shapes and other features. I will amplify published summaries (Owen-Smith 1975, 1988) with additional information from my doctoral thesis (Owen-Smith 1973).

Social structure

The social organization of white rhinos in the wild is structured by a mosaic of territories, each occupied by a dominant territorial bull, plus perhaps one or more subordinate adult males. Females accompanied by calves, and sub-adults (males $\leq$ 10 years and females $\leq$ 7 years of age) range through the territorial mosaic. The annual home range of a cow encompassed 6-7 male territories, but most cows spent over half their time during the wet season within one or the other of two adjacent territories. Unless otherwise specified, the term "bull" refers specifically to a dominant territory-holder (or so-called α-male).

Pre-mating consort period

Upon encountering a female white rhino within his territory, a territorial male commonly approached to confront the cow from a few meters away downwind. Approaches were commonly accompanied by a hiccing sound. Cows responded with snorts or gruff snarling roars, sometimes accompanied by advancing steps, which served as defensive (or space-maintaining) threats. After perhaps a minute, the bull usually moved off. Sometimes he remained, commencing grazing or some other activity in the vicinity of the cow.

Persistent accompaniment of a cow by a bull over a period of several days was a reliable indication that the cow was about to come into estrus. All associations that were closely monitored eventually led to courtship and mating. All observed matings, except one in unusual circumstances, were preceded by a consort period. The likelihood of a cow being accompanied by a bull varied with the reproductive stage of the cow. Cows known (from subsequent parturition) to have been pregnant were seen together with a bull on only 2.5% of sightings (N = 728). Cows with calves under six months of age had a bull in attendance on only 1.6% of days seen (N = 186). None of these associations lasted longer than a day or two. Cows that were neither pregnant nor less than 6 months post-partum were accompanied by a bull on about half of the days when they were observed, as a year-round average.

Estimating the duration of the consort period required locating specific animals almost daily, prior to as well as through the consort period, until the day of mating. Hence in some cases only a minimum duration, or a possible range, was obtained. Based on 10 case histories, the consort period varied between reliable extremes of 4 and 20 days (Table 1).

During most of the consort period, the cow being attended showed no physical or behavioral signs of estrus. She deterred any approaches by the bull closer than about 10 m, by making threatening snorts or roars. Occasionally cows advanced to clash horns with the bull with a roar. Such threats by the cow occurred on average 2.3 times per hour. Otherwise cows ignored the bull's attendance. The bull merely followed after the cow as she grazed or walked, usually within 10-20 m. When the cow lay down, the bull backed in closer to lie at a mean separation of 10 m (range 2-20 m). If the cow defecated or urinated, the bull waited until she had moved on, then sniffed carefully at her dung or urine. He raised his upper lip in the "flehmen" response. Occasionally bulls made a few hiccing sounds while moving nearer to a cow after having become separated. Such actions occurred on average once per 5 hours of observation. In instances when a bull had lost contact with a cow, he searched agitatedly until he had tracked her down, generally by following her scent trail.

When the direction of movement of the cow brought her into the vicinity of a territory boundary, the bull commenced making soft squeals, positioning himself between the cow and the boundary. If the cow persisted in moving towards the boundary, the bull moved round squealing, to block her progress. He horned the ground, scraped with his feet, and urinated in sprays at short intervals. On one occasion 29 spray-urinations were recorded within 122 min in such circumstances. If the cow tried to move past, the bull circled squealing and wailing to place himself between her and the boundary again. Cows reacted to such maneuvers with threatening snorts, roars and advancing steps. The noise associated with such "quarrels" was audible from some distance, and frequently drew me to the scene. However, other rhinos, including neighboring territorial bulls, did not seem to react.

Territory boundary blocking interactions took place on average every 3.5 hours (N = 100 hours) while the rhinos were active (grazing or walking). The frequency depended on the size of the bull's territory, and the attractiveness of its grazing. Some interactions were brief, while others persisted for an hour or two. In most cases, the cow eventually gave up her attempts to proceed, and moved back towards the core of the territory. In a few instances when my presence caused the cow to run off, the bull raced after her at a trot to get in front again. In one extreme case, a bull blocked all attempts by a cow to cross out of his territory from 07:30 in the morning until 17:00 in the late afternoon. The cow finally escaped over the boundary when I disturbed the animals.

Once a cow had crossed more than 100-200 m into a neighboring territory, the bull gave up following. On rare occasions, generally in the vicinity of waterpoints visited by many rhinos, a cow was able to transfer between territories while two neighboring territory holders engaged in a border confrontation. Most of the time, the bull successfully prevented the cow from exiting from his territory. Hence usually the cow was accompanied by the same bull for the duration of the consort period.

Territory boundary blocking maneuvers by the bull confined within his territory not only the cow, but all accompanying rhinos. Where a cow had a sub adult female companion, I could not tell from the behavior of the bull which of the females was approaching estrus. The bull also tolerated the presence of sub adult males (generally aged 3-6 years, but in one case a 10-year-old male approaching maturity).

In the few instances when subordinate adult males accompanied cows for a day or two, the cows were no more or less threatening than to territorial male consorts. Cows sometimes had as companions sub adult males aged up to 9 years, but the presence of the latter was ignored both by the cow and by the accompanying territory holder.

In a single exceptional case, a subordinate bull mated with a cow, with no preceding or subsequent consort period. The cow was accompanied by a calf only five months old, so this was

probably her first post-partum estrus. The mating was not fertile, since the cow came into estrus a month later, and was accompanied by the territorial bull on this occasion. This may have represented a "silent heat".

Estrus

The onset of estrus was indicated by the commencement of regularly repeated advances by the bull, accompanied by a wheezy hiccing sound. This active courtship began about 24 hours prior to copulation (Table 1). Between 24 and 16 hours before copulation, approaches by the bull occurred at a rate of 2-4 times per hour. Their frequency increased during the last few hours before mating to between 5 and 21 times per hour.

During the early stage of courtship, cows reacted to each approach with defensive threats. The bull then halted and moved away. During later stages, cows responded to the bull's advances by emitting little squirts of urine. Bulls commonly sniffed at the urine patch on the ground, and on occasions placed their noses under the cow's tail to sample the urine directly. Over time a cow's defensive reactions to the bull's advances weakened. Some cows seemed to solicit approaches, by walking a few steps then standing waiting.

The bull made first contact with the cow by ignoring her threats, advancing slowly with hiccing noises to rest his chin on the cow's rump. At first cows responded by warding off such contacts, but eventually the head-on-rump position was tolerated. This led to mounting attempts by the bull. Several mounts were generally made before bulls achieved intromission. Copulations lasted between 15 and 30 min, with multiple ejaculations.

As is apparent, courtship is a slow-moving affair drawn out over 24 hours. Cows are initially defensive, but over the course of time show diminishing resistance. Estrus behavior involves little more than tolerating a bull's advances, plus emitting urine squirts when approached. Bulls seemed to delay mounting attempts until some chemical signal received from the cow's urine indicated that the timing was right.

During the consort and courtship periods, bulls showed a "condescending subordination" towards the cow, as well as her companions. Bulls hastened away when cows threatened strongly, yielded to the cow's chosen path of movement, and were sometimes displaced by a cow from their chosen resting site. Nevertheless, when a cow approached a territorial border the bull asserted his dominance, although even then almost "apologetically". Such behavior seems designed to ensure that cows remain within the bull's territory until receptive to mating.

Bulls usually stayed with cows for 1-5 days after the day of mating (Table 1). Except in one instance, bulls ceased further advances after copulation had occurred. In the exceptional case the bull was forced off the cow by an overhanging tree 10 min after copulation had commenced, and a second mating occurred 3 hours later. In one an old bull seemed impotent. He mounted the cow six times over the course of six hours, achieved an erection on some occasions, but did not attempt intromission. The following day only four hiccing approaches were observed during 8 hours observations, all checked by snorts from the cow. In one instance when a subordinate bull attempted to mount a cow a few hours after she had been mated by the territorial bull, the cow threw him off so violently that he landed on his side.

Estrous cycle

Some cows were seen being accompanied by a bull for a single consort period only, suggesting that mating was successful at first attempt. In other cases cows were accompanied by various bulls over a period of several months. Because individuals could not be located regularly, it was difficult to establish the estrous cycle duration with any precision.

One sub-adult (post-pubertal) female was seen being courted 72 days after she had previously been mounted by a bull. Another sub-adult female was seen being mounted on two occasions 162 days apart, but had been accompanied by other bulls in the interim. One adult female gave birth 18 months 3 days after she had been mated. Since reliable records indicate a gestation period of 16 months, this indicates an interval of about 63 days between the observed mating and the one that had resulted in conception. Based on interpreting consort periods, there were 3 cases where a cycle duration of about 30 days was indicated, 4 cases where it seemed to be 60-65 days, and one case (involving a sub-adult female) where a duration of about 40-45 days was suggested. However, for all of the longer intervals, the female concerned had not been seen in the intervening month, so that a 30-day cycle could not be excluded. These observation appear consistent with a *ca.* 30 day cycle duration, which may be suppressed in some months.

Seasonality of estrus

Records of cows being accompanied by bulls show a peak in the summer wet season period from November to February, and a low during the winter dry season months of July - September. Calving records show a peak over March - July, corresponding with the gestation period of 16 months. This suggests that most females underwent only one or two estrus cycles before conceiving. However, rainfall patterns were erratic during my study period. Some females come into estrus following late rains through March-June so that a few calves were born during the late dry season period from August to November (Owen-Smith 1988).

Detailed annual patterns of consort behavior suggest that estrus is stimulated by a flush of green grass following rains, and suppressed when dry conditions lead to mainly brown grass (Fig. 1). In 1966 heavy rain fell through January, followed by a dry period, then further light rain in late March and April brought on a flush of green grass through April-May. The main consort peak occurred in January-February, with a few cows being accompanied by bulls through April-June. In the 1968/9 season, little rain fell until early December, then there was a midsummer drought broken by good rains in March. The peak consort period was delayed until February-March, tapering off thereafter. In 1969/70 drought conditions prevailed, so that consort associations varied erratically with an early peak in December and a late peak in June. In 1970-71 there were good early summer rains, then a short summer drought, followed by good late rains in April and May. Peak consort levels occurred in November, February and April-May.

The pattern suggests that estrus cycling was initiated a week or two after a flush of green grass, which in turn occurred 1-2 weeks after rain. Following matings, the number of cows that were estrus-ready tapered off. Late rains then induced estrus among cows that had not been susceptible earlier. If these cows did not come into heat then, they did not cycle until the following rainy season.

The birth sex ratio of the white rhino calves born during and subsequent to my study was strongly male-biased (173:100, N = 139). However, the sex ratio of adults plus sub-adults was close to parity, while white rhinos introduced from Umfolozi into other parks show more female than male births (Owen-Smith 1988). Analysis indicated a tendency for males to

predominate following short inter-calving intervals, with relatively more females born following long calving intervals. Also, primiparous females produced mainly male offspring, while old cows produced mainly daughters, but the age of the mother was also related to the inter-calving interval.

Discussion

Three features of white rhino reproduction seem to be unusual: (i) the timing of the birth peak during the dry season, (ii) the long duration of the pre-mating consort period, and (iii) the variable male bias in the birth sex ratio. These could possibly be of significance to the problems that have been experienced with captive breeding.

Because the monthly occurrence of consort periods and births varied widely between years, there is clearly no seasonal control on reproduction through day length. Instead, proximate nutritional factors acting on estrus cycling seem to be responsible for the seasonal pattern of births. African elephants likewise show conception peaks following peak rainfall months (Hanks 1969; Laws *et al.* 1970). For elephants with a 22-month gestation, calves are also born during the early part of the rainy season. For white rhinos, calves are born during the early dry season following a 16-month gestation. This may seem selectively disadvantageous, given the high nutritional demands of lactation. However, body reserves built up by the mother during the preceding wet season could help sustain lactation through the dry season months.

This raises the possibility of a "flushing" effect, i.e. stimulation of estrus by a rising nutritional plane, as is known for sheep. Conversely, estrous cycling could be inhibited, or become erratic, if forage quality is too low.

Before forming a consort relationship, bulls evidently detect that the female is a candidate for estrus, i.e. neither pregnant nor in post- partum anestrus. However, under dry conditions when food quality is poor, bulls do not form persistent associations with cows, so that the appropriate signal must then be lacking.

Cows should be able to associate the smell of the accompanying bull with the odor of his scent marks (dungheaps and spray-urination sites) defining the territory. Some cows seen being courted were strangers to the study area, while others were familiar residents. Cows become accustomed to the continual presence of the accompanying during the consort period. More active behavioral stimulation occurs during the territory boundary blocking rituals, which occur several times per day.

Although mate choice by female white rhinos seems passive, their behavior nevertheless leads to effective mate selection. Cows were almost invariably joined by males that had been successful in intra-male competition for territories. They tested the physical fitness of such males by persistently attempting to move across territory boundaries. A male becomes a sire only if he is successful in keeping the female within his territory for one or more weeks.

White rhinos living at lower population densities can show considerably larger territories than those prevailing at Umfolozi during my study: 50 km^2 or more, versus 0.7-2.6 km^2 (Meister & Owen-Smith in press).

Boundary blocking interactions would occur much less frequently than I documented at Umfolozi. Although reproduction occurs successfully, inter-calving intervals seem to be somewhat lengthened compared with those in the Umfolozi population (Owen-Smith 1988).

Whether the delay in the onset of pregnancy is due to less favorable nutrition, or to a lowered behavioral stimulation of females, is the interesting issue.

Subordinate adult males have their reproductive behavior suppressed by the presence of the dominant territory holder. This presence is manifest by scent as well as through repeated direct confrontations. Females that are potentially ready for mating may have their estrous cycling released by the presence of such males, or not released when the appropriate signals are lacking. This sensitivity may help explain why the estrous cycle appears so erratic in duration. Although the basic cycle duration appears to be about 30-35 days, a cycle may not be manifest when conditions are wrong. Some of the lengthened cycles could result from early death of the fetus. The early fetal mortality could even be adaptive, allowing females the potential, through sex-biased mortality, to exert some control over the sex of their offspring relative to the prevailing circumstances (Owen-Smith 1988).

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TABLE 1 Data on oestrus and mating

	Date	Age category of female	duration of consort period * pre-mating (days)	post-mating (days)	total (days)	courtship duration (hrs)	no. of mounts before copul.	duration of copul mounted (min)	intromis (min)
1	Mar. '66	Subadult	11+	3	15+	10+	-	-	-
2	Mar. '66	Subadult	10-24	4	15+	-	-	-	-
3	June '66	Adult	20	5	26	25+	7+	-	-
4	Dec. '68	Adult	13-14	5	18-19	16+	2+	24	20
5	Nov. '69	Adult	4	5-16	10-21	(17)	2+	23	15
6	Apr. '70	Adult	8-10	3	12-14	<17	-	(22)	(10)
7	Nov. '70	Adult	-	-	16-20	-	-	-	-
8	Nov. '70	Adult	-	-	-	24	-	26	24
9	Jan. '71	Subadult	3+	2	6+	-	5+	-	-
10	Jan. '71	Subadult	6+	2	8+	-	-	-	-
11	Jan. '71	Adult	6-9	6	13-16	-	-	-	-
12	Jan. '71	Adult	17+	12+	29+	-	-	-	-

* ranges shown are between minimum and maximum estimates (bracketed) - minimum duration

figure 1. Seasonal variation in oestrus levels correlated with monthly rainfall and grass greeness.