Dr. T. Mann, Dr. R. M. Laws and Mr. J. M. King kindly read the manuscript and made a number of helpful suggestions.

REFERENCES

- EDGAR, D.G. (1953). The progesterone content of body fluids and tissues. J. Endocr., 10;
- FERRIER, A. J. (1948). The care and management of elephants in Burma. Steel Bros. & Co. Ltd., London.
- KUHME, W. (1963a). Ergänzende Beobachtungen an afrikanischen Elefanten (Loxodonta africana Blumenbach 1797) im Freigehege. Z. Tierpsychol., 20: 66.
- (1963b), Ethology of the African elephant (Loxodonta africana Blumenbach 1797) in captivity. Int. Zoo Yb., 4: 113.

- PERRY, J.S. (1953). The reproduction of the African elephant, Loxodonta africana. Phil. Trans. R. Soc., B 237: 93.
- (1964). The structure and development of the reproductive organs of the female African elephant. Phil. Trans. R, Soc., B 248: 35.
- SHORT, R. V. and BUSS, I. O. (1965). Biochemical and histological observations on the corpora lutea of the African elephant, Loxodonta africana. J. Reprod. Fert., 9: 61.
- SHORT, R. V. and KING, J. M. (1964). The design of a crossbow and dart for the immobilisation of wild animals. Vet. Rec., 76:
- SLADE, H. (1903). On the mode of copulation of the Indian elephant, Proc. zool. Soc. Lond., 1: 111.
- WRIGHT, A. (1964). Mating habits of elephants. Afr. wild Life, 18: 301.

Author's address: R. V. Short, Department of Veterinary Clinical Studies, Madingley Road, Cambridge, England.

(Received for publication October, 1965)

MATING AND COURTSHIP OF THE BLACK RHINOCEROS (DICEROS BICORNIS L.)

John Goddard, Biologist, Ngorongoro Conservation Area

SUMMARY

During a study of the rhinoceros population at Ngorongoro Crater and Olduvai Gorge, mating or courtship behaviour was observed on six occasions. Pre-copulatory, copulatory and post-copulatory behaviour is described and illustrated. Mating takes place at any time of the year and there is little doubt that the species is polygamous and polyandrous. The impermanence of the mating bond, and the pugnacity of the male rhinoceros when a female is in oestrus, is shown with the aid of a documented description.

INTRODUCTION

The black rhinoceros possesses certain characteristics which enable an observer to recognise an individual if close-up photographs of the rhinoceros are available. Normally, when studying the habits and ecology of a wild animal, it is necessary to mark or tag individual animals so that they may be recognized when seen again at some subsequent date. This is not necessary with the rhinoceros, as is the case with several other species of African mammals. Characteristics used for identification of a rhinoceros are the sex of the animal, the size and shape of the anterior and posterior horns, peculiarities of the ears, and the pattern of wrinkle contours on the snout.

In 1963 Dr. Hans Klingel, formerly of the Serengeti Research Unit, used the technique of horn and ear identification on part of the rhinoceros population at Ngorongoro Crater, recording 26 animals (see Turner and Watson, 1964). Identification by horns alone can be misleading, especially among rhinoceroses with relatively small horns. In any time of the day.

addition some rhinoceroses, especially those with thin rapier-like horns, break their horns, making identification uncertain. In such cases it was found that the pattern of wrinkle contours on the snout can be a considerable aid to positive identification.

By using this technique of identification it has been proved that at least 78 rhinoceroses use Ngorongoro Crater as a suitable part of their habitat at some time of the year. An additional study area that is bisected by the world-famous Olduvai Gorge also shows that at least 60 rhinoceroses occupy the area immediately adjacent to part of the Gorge. Preliminary results suggest that in most areas of the Ngorongoro Conservation Area the rhinoceros population is considerably higher than was formerly believed.

In the sample of 78 rhinoceroses which live in, or immediately adjacent to Ngorongoro Crater, I have observed mating or courtship behaviour of the rhinoceros on six occasions during a period of 19 months (March 1964 - September 1965). Using the identification technique described above some interesting records of the social relationship among rhinoceroses have been collected.

MATING SEASON

Ritchie (1963) states that mating takes place at any time of the year, although he does not present specific data to support his statement. Certainly the data shown in Table 1, collected in Ngorongoro Crater over the years, tend to support Ritchie's statement. Mating will apparently take place at

MATING BEHAVIOUR

(a) Precopulatory behaviour

In pre-copulatory behaviour the male rhinoceros is not aggressive and the primary succession of events appears to be governed by the female. The female will sometimes walk considerable distances, and the male follows closely behind her. When she stops to feed or to rest the male commences to show an active interest. The pair will frequently stand facing one another periodically "jousting" with the anterior horns (Figure 1), or gently nudging one animal.

another with the side of the head. Occasionally the male will thrash his head from side to side, scraping the front of the anterior horn and upper lip against the ground in a wide sideways sweeping motion. He may advance with a stiff-legged gait, keeping the hind legs rigid and dragging them on the ground. This behaviour can be observed during other periods, when a male rhinoceros meets a female, and it is occasionally seen prior to defecation at a well-used dung pile. The male frequently jabs the female between the front legs or the hind legs, and sometimes underneath the "barrel" of the

TABLE 1 Table showing mating dates of rhinoceros in Ngorongoro Crater

(actual and calculated)

		A contract of		
No.	Rhinoceros involved	Date of mating	Time of day	Observer
1		January, 1959		G. Harvey
2*	—	July, 1953	<u> </u>	J. R. A. Hewlett
3*		August, 1954		J. R. A. Hewlett
4*	Q.	July, 1963	_	J. Goddard
5*	Ο.	December, 1963		J. Goddard
6*	F.	March, 1964	. —.	J. Goddard
7	В, L.	16 April, 1964	4.10 p.m.	J. Goddard
8	A, E.	23 June, 1964	3.45 p.m.	J. Goddard
9	V2, L.	7 April, 1965	1.00 p.m.	J. Goddard
10	M, L.	7 April, 1965	4.15 p.m.	J. Goddard
11	P, T1 ,	19 August, 1965	10.00 a.m.	J. Goddard
12	P. T1 ,	17 September, 1965	7.40 a.m.	J. Goddard

^{*} Date of mating is calculated assuming a gestation period of 540 days (Morris and Jarvis, 1959). Nos. 2 and 3 were based on Hewlett's records of observations of new-born calves. In Nos. 4-6 the birth day of the calf is known to the nearest two weeks. Numbers not marked with an asterisk are actual observations of mating rhinoceroses.

The capital letters refer to the particular rhinoceros in my catalogued records.

During oestrus the female, whether tack him when he dismounted. On anfeeding or resting, urinates frequently. The male invariably sniffs the deposit and exhibits the "Flehmen" position by which he tests the receptiveness of the female. The neck of the male is raised upward and backward, and the upper lip curls up in a snarl-like expression (Figure 2). The male may approach the female from the side jabbing her in the ribs with his anterior horn and forcing her to move in a tight circle.

Prior to mounting the male rests his chin on the caudal base of the female (Figure 3), and pushes his head along her spine until the ventral part of his neck rests on her caudal base. Using his neck as a lever he raises his forefeet off the ground and drags his brisket along the spine of the female (Figures 4 and 5). The forefeet are then placed behind the shoulder of the female and the male raises himself to the position shown in Figure 6. This position, usually with the tail raised is the characteristic posture for long periods of time prior to copulation. The male stands in this position for periods of up to ten minutes with no attempt at copulation, until he is dislodged by the female. Mounting, and taking up of the position shown in Figure 6, may extend over several hours and occur as many as 20 times before copulation is attempted. The period between mountings is usually taken up by active feeding or walking.

Ritchie (1963) notes "that mating is almost always preceded, and usually succeeded, by violent attacks on the bull by the cow." This is by no means always the case. Only in one instance out of my six observations did the female attack the bull prior to mating. In this display the male approached the female extremely cautiously, taking short steps, and occasionally displaying the sideways sweeping motion of the head described above. At a distance of about five yards the female charged him viciously, emitting the characteristic "puffing snort". The male ran off and always galloped in a small circle, and then commenced the extremely cautious. short step approach once again. When he finally mounted her she did not at- ism of the rhinoceros during mating

other occasion the female involved made no attempt to attack the male prior to mounting, but each time he dismounted she charged him viciously. The male always retreated in the onslaught of these attacks. On all other occasions the female made no attempt to attack the bull either prior to, or after, mounting.

If the female is accompanied by a calf, or another immature animal which may not be her calf, the latter appears completely indifferent to the entire proceedings (see Figures 6 and 7), if the association between the male and female has been of a relatively long duration. A male that has just encountered a female in oestrus is regarded with suspicion by the calf, and may be charged by it, the male usually retreating in the face of the charge. After the male has apparently been accepted by the female, the calf or immature animal accompanying her takes little further interest in the intruder. Other species which may be in the vicinity, such as the wildebeest (Gorgon taurinus Thomas) or spotted hyaena (Crocuta crocuta Erxleben), take an intense interest in the courtship activities.

(b) Copulation

Prior to copulation the male presents the position shown in Figure 6 and then by a "rowing" motion drags himself along the back of the female. Copulation follows with the female stationary and the male either in the position shown in Figure 7 with the body arched high into the air, or as in Figure 8 with the chin almost resting on the shoulders of the female. The tail of the male is usually held down during coitus.

Copulation is an extremely prolonged affair as the data in Table 2 will show and is undoubtedly one of the major reasons for the legend, cultivated among certain races, of the aphrodisiac powers of various parts of the rhinoceros.

Several authors (Bramwell, Hewlett, 1958) have referred to the loud vocal-

TABLE 2

Table showing data on the copulation of the black rhinoceros

Observation No.	Location	Date	Time of coitus	Observer
1 .	Murchison Falls Nat, Park	March, 1955	36 min.	F. Poppleton
2	Ngorongoro Crater	16 April, 1964	32 min.	J. Goddard
3	Ngorongoro Crater	17 September, 1965	29 min.	J. Goddard

and courtship, but this apparently occurs only with certain individuals. In my observations the males involved were silent during the entire ceremony. However the female periodically emitted a low pitched squeal during coitus.

(c) Post-copulatory behaviour

After coitus the male frequently attempts to stay mounted, as in the position shown in Figure 6, but the female usually walks away and dislodges him. When copulation is completed the female may lie down or commence to feed actively, while the male usually feeds actively. If she lies down the male may attempt to make her get up by jabbing her with his anterior horn, or he may simply lie down beside her.

Spinage (1962) expresses the opinion that a male rhinoceros may remain attached to a female after mating. The pair shown in Figure 3 mated on April 16th, 1964 and remained attached for four months, after which the male took up a solitary existence. The pair shown in Figure 8 were seen displaying courtship behaviour on August 19th, 1965 but five days later the male had left the female. Exactly one month later the same pair were seen mating, and the day after copulation the male left the female, and has not been attached to

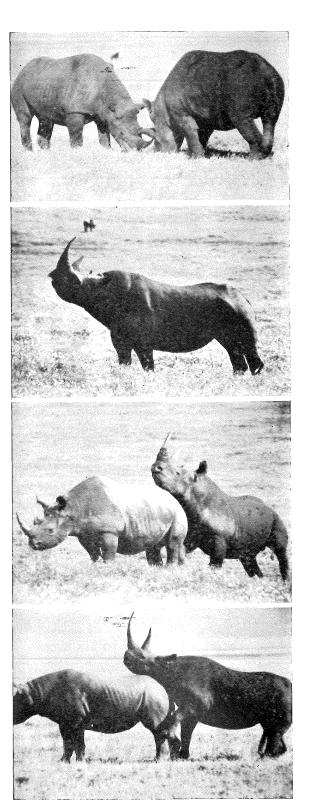
her up to the present date (November, 1965). The data collected suggests that the mating bond is by no means permanent, and is governed to a large extent by the size of the home range of the male, and the extent to which the female in oestrus uses that home range.

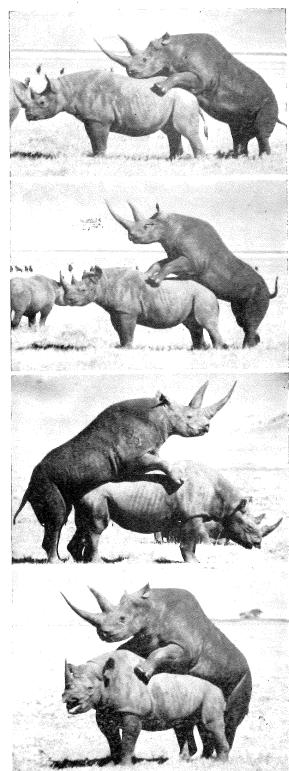
POLYGAMY - POLYANDRY

There appears to be little doubt that the species is polygamous and polyanrous Ritchie (1963) cites the observations of M. Cowie, Director of Kenya National Parks. Over a 22 month period I have seen several male rhinoceroses in company with several different females, the association lasting several weeks or a few days, depending on the movements or attitude of the female. Mating would undoubtedly occur if any of these females came into oestrus. The pair shown in Figure 3 mated in April, 1964 and twelve months later I saw the same female mounted by two other males during a six-hour period.

COMPETITION BETWEEN MALES

In conclusion I should like to cite the following incident which I observed in





Opposite: Figures 1 - 4 (left) and 5 - 8 (right). For explanation see text.

Ngorongoro Crater on April 7th, 1965. remaining silent. It describes the pugnacity of the male rhinoceros when a female is in oestrus and illustrates the impermanence of the mating bond. At 12.10 p.m. I observed a female with a female calf, accompanied by an adult male. Both these animals were in the confines of their habitual home range at this time of year. The female walked toward a stream bed, closely followed by the male, and both she and the male fed actively in the stream bed for one and a half hours. During this period the male mounted her, but made no aggressive attempt at copulation. At 1.45 p.m. the female left the stream, closely followed by the male. At 2.30 p.m. both animals passed the usual boundary of their home range, and at 3.45 p.m. the female walked towards a second adult male. When the female was approximately 30 yards from the second male, the latter became aware of her presence and walked toward her. Immediately the first male charged the second male viciously, his ears flattened, upper lip contorted, and emitting a ghastly puffing shriek. The second male was silent, but retreated in the face of the charge.

Approximately 200 yards from the group a third male was sleeping. The puffing shrieks of the first male awoke him and he immediately got up and rushed over to the group. The female walked away closely followed by the second male. The first male rushed out and charged straight at the third male with exactly the same behaviour described when he approached the second male. Both animals rushed together and halted approximately five yards from each other. The first male advanced slowly but the third male remained motionless. The first male then rushed forward and they jousted with the anterior horns, trying to club one another on the side of the head. At each charge (always precipitated by the first male) the other animal would defend, the former always emitting puffing shrieks, but the latter on all occasions the data shown in Table 2.

Periodically the third male walked sideways to the other animal with the stiff-legged display described in the earlier part of this paper. In this pattern the front legs are held rigid, and the animal shuffles forward, alternately dragging the hind legs. Defecation invariably follows this display, accompanied by the sideways sweeping motion of the head with the upper lip and anterior horn in contact with the ground.

The third male then advanced on the first male who once again charged. Actual contact with one another was infrequent, one or the other usually backing up slowly, occasionally jerking their heads upward and down in a "rooting" motion with the anterior horn. This aggressive behaviour between these two males was still going on when I left the pair at nightfall.

The female and the second male had retired to a distance of about 100 vards from the other two males. The second male approached the female with the cautious short step approach described above and the female periodically charged him. A "joust" with the anterior horns followed as is shown in Figure 1. Immediately following the joust the second male wheeled around and always galloped in a small circle to stop and return to the female with the cautious, short step approach. The second male finally mounted the female but despite subsequent mounting did not copulate. The following day, April 8th, both the first and the third males had taken up a solitary existence in their usual home range. The female and the second male were in close association, but on April 9th they had separated, the male returning to his usual haunts. He has not been seen with her up to the present date (November, 1965).

ACKNOWLEDGEMENTS

I should like to thank Mr. F. Poppleton for his permission to use part of

REFERENCES

BRAMWELL, P., HEWLETT, J. R. H. et al. (1958). Tanganyika Game Department Rhino survey. Unpublished manuscript. Typewritten, 4 pp.

MORRIS, D. and JARVIS, C. (Editors) (1959). The International Zoo Yearbook, Volume 1. Zool. Soc. Lond.

RITCHIE, A. T. A. (1963). The Black Rhinoceros. E. Afr. Wildl. J. 1: 54-62.

SPINAGE, C. A. (1962). Animals of East Africa. 1st ed. Collins, St. James Place. London.

TURNER, M. and WATSON, M. (1964). A census of game in Ngorongoro Crater. E. Afr. Wildl. J., 2: 165-168.

Author's address: John Goddard, Biologist, Ngorongoro Conservation Area, P.O. Box 3102, Arusha, Tanzania.

(Received for publication December, 1965)