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Breeding Behavior in Captive Indian Rhinoceros

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With 6 Figures

Introduction

The historical background, initial breeding, and the first birth of a pair of Indian rhinoceroses, *Rhinoceros unicornis*, at the National Zoological Park have been reported elsewhere (Buechner et al. 1975). More detailed descriptions of the reproductive behavior are given in the present paper. The events leading to successful copulation are of interest in that both animals were sexually inexperienced and required considerable orientation as a prerequisite to mating.

On arrival at the zoo, the ♂ ("*Tarun*") was about 2.5 years old and the ♀ ("*Rajkumari*") was 6 months old. The first attempt to mate occurred on 9. 8. 1970, when the ♂ and ♀ were 12.8 and 7.3 years of age, respectively; the second and third attempts occurred on 26. 8. 1971 and on 12.—13. 8. 1972. The first 2 attempts were curtailed around midnight after 9—14 hours of sexual activity; in August 1972 the animals were allowed complete freedom of access to one another throughout the ♀'s period of receptivity (20 hrs). None of the mounts exceeded 15 minutes in any of these 3 initial attempts to breed. The ♂ achieved partial intromission only occasionally. The penis (ca. 1 m long) usually passed beneath the ♀ or laterally, mostly because the ♂ positioned himself too far forward on the ♀'s back. When the ♂ was in the proper position for insertion, the penis was ineffective in reaching the vagina.

On 30. 9. 1972, the ♂ mounted the ♀ quickly, intromitted without difficulty, and remained mounted for 70 minutes, with frequent bouts of pelvic thrusting. Conception occurred on this date, and a ♂ calf was born on 30. 1. 1974.

The experiences at other zoos also indicate that a long period of orientation is required for immature Indian rhinoceroses prior to successful copulation. At the Basel Zoo, the ♀ went through 19 periods of observed estrus before conception occurred, and the initial breeding was accomplished by keeping the ♂ and ♀ together throughout the night whenever the ♀ was in estrus (Lang 1961).

Schedules of placing the ♂ and ♀ together seem to be important in achieving synchrony of sexual motivation and opportunity for initial copulatory orientation. Complete separation for prolonged periods (ca. 6 mos.) may be as essential as around-the-clock access of the animals to one another during seasons of the year favorable for conception in the North Temperate Zone.

Breeding Behavior in 1972

Observations of the ♂ and ♀ during "*Rajkumari's*" proestrus, throughout one estrous period without copulatory success, and through the subsequent onset of estrus leading

to successful mating 48 days later show the manifestations of disposition to mate and contact-promoting interactions in relationship to the ♀'s estrus (Fig. 1 and 2). Although the daily observations varied somewhat in duration and time of day, the behavioral patterns of these 2 Indian rhinoceroses, neither of which had bred previously, are clearly depicted.

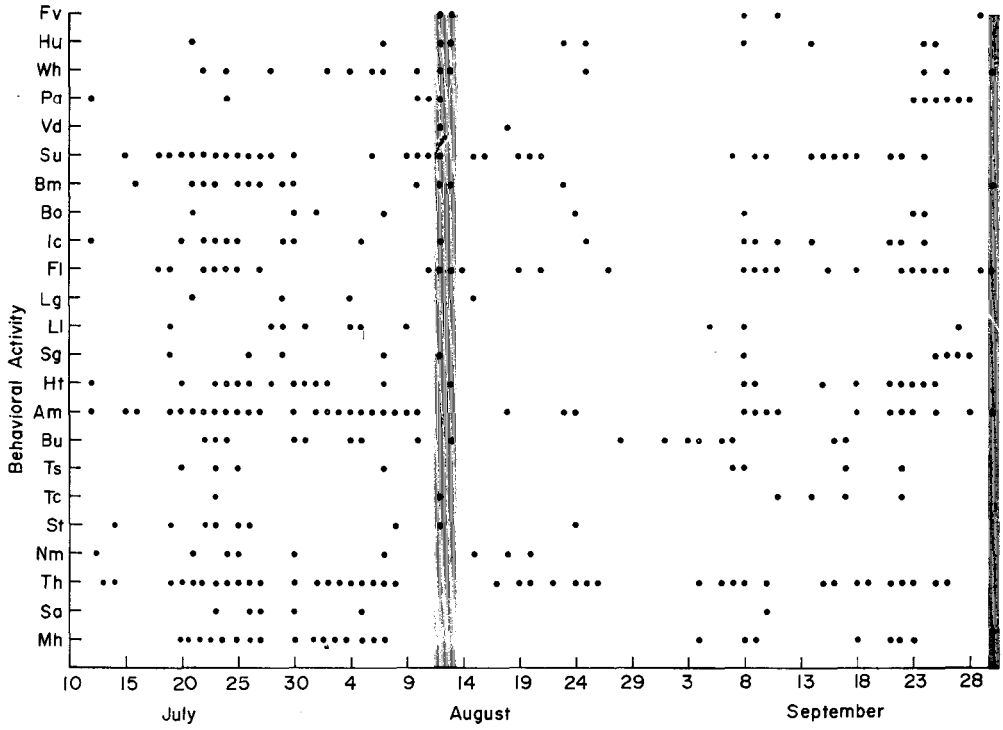

Fig. 1. Pattern of "*Rajkumari's*" behavioral activities during the onset of 2 periods of estrus (vertical shaded lines) in 1972. Vf = vulval flashing, Hu = horizontal urine squirting, Wh = whistling, Pa = pacing, Vd = vaginal discharge, Su = squirt at end of normal urination, Bm = backing into ♂, Bo = backing into objects, Ic = invitation to chase, Fl = Flehmen, Lg = licking ♂'s genitalia, Ll = licking ♂'s leg, Sg = smelling ♂'s genitalia, Ht = head tossing, Am = approaching ♂, Bu = brown material in urine, Ts = tail swishing, Tc = tail muscle contraction, St = stroking ♂ with chin, Nm = nuzzling ♂ with prehensile lip, Th = threatening ♂, Sa = salivation during head-to-head encounters, Mh = mutual horn rubbing

Behavior of the ♀

Apart from her interactions with the ♂ "*Rajkumari*" exhibited several behavioral and physiological signs of the onset of estrus, such as vaginal secretions, vulval flashing, urine-squirting, and whistling. However, none of these indications alone, or even in combination, could be used to predict precisely the time of full overt estrus and readiness to accept mounting by the ♂. Only when the ♂ mounted the ♀ could we be certain that the ♀ was in estrus. These signs of estrus have been reported by Schenkel and Lang

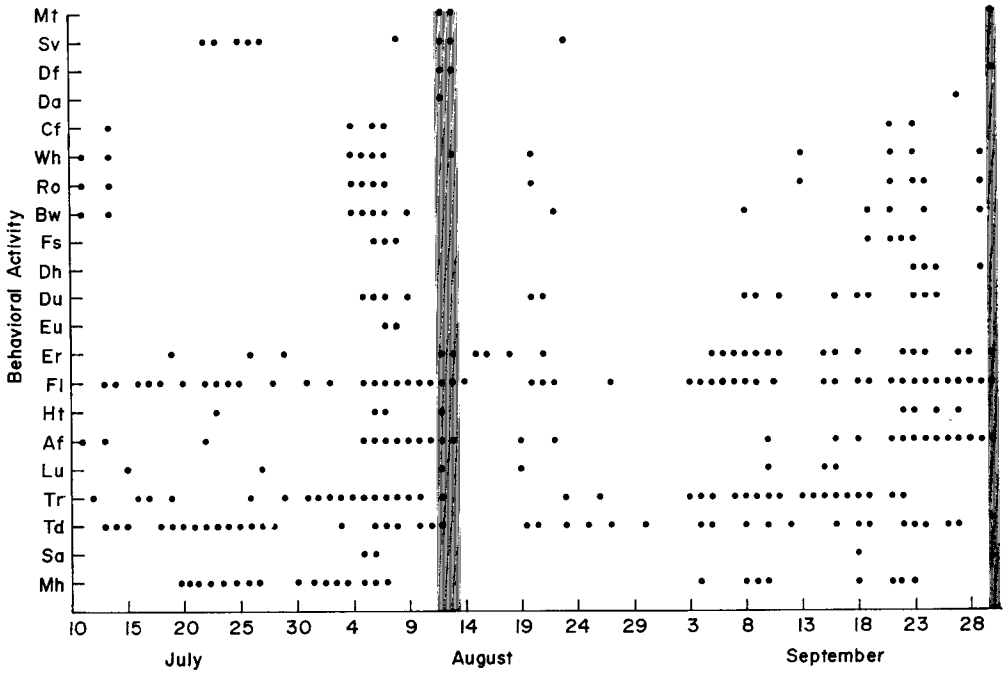

Fig. 2. Pattern of "*Tarun's*" behavioral activity in relationship to the ♀'s estrus (vertical shaded lines) during the summer of 1972. Mt = mounting, Sv = smelling vulva, Df = driving ♀, Da = dance, C = chasing ♀, Wh = whistling, Ro = roaring, Bw = banging wall, Fs = Flehmen with simultaneous urine squirting, Dh = dragging hind feet, Du = drinking ♀'s urine, Eu = eating hay soaked in ♀'s urine, Er = erection, Fl = Flehmen, Ht = head tossing, Af = approaching ♀, Lu = long urination, Tr = testes retracted, Td = testes descended, sa = salivation during head-to-head encounters, Mh = mutual horn rubbing

(1969) for the Indian rhinoceros, but without detailed reference to the total time-period over which they occur or to the exact time of mounting. Mucous secretions, vulval flashing, and urination, as described briefly by Anderson (1969) and Nishikawa and Hafez (1968), are also indicators of estrus in the mare; and they reveal the evolutionary link between these 2 perissodactyla.

The first positive sign of "*Rajkumari's*" mid-August estrus was a milky vaginal secretion observed at 14.55 hours, about 2 hours prior to the first mount. Flashing the vulva, rhythmic contractions in which the partly everted and swollen labia minor are visible momentarily, was first observed when the ♀ was halfway through the 15-hour period over which she accepted 23 mounts by the ♂. Isolated spontaneous horizontal squirting of urine, supposedly a good indicator of the onset of estrus (Schenkel and Lang 1969), was seen only on 21. 7. (1 squirt) and 7. 8. (4 squirts) before the first estrus occurred on 12. 8. 1972. When she was in full estrus, "*Rajkumari*" emitted at least 20 horizontal urine squirts, often coupled with vulval flashing. On 4 separate days after the August estrus, a few single horizontal squirts were observed; then unexpectedly on 24. 9. a series of 25 squirts occurred over a 48-minute period (01.39—02.27) — a week prior to the complete copulation. The following night 6 squirts were observed, again over

a brief period between midnight and 03.00; no horizontal urine squirts were seen thereafter, even on the day of copulation.

Whistling was heard occasionally before and during the first estrus, and infrequently thereafter. Immediately after copulation the ♀ emitted a series of frequent, high-pitched, subdued whistles, which suggests that whistling is an expression of a high state of excitement.

Backing into objects, such as a stump, wall, or the bars of a cage, provided a good index to the ♀'s interest in breeding. Similarly, Flehmen [upcurling of the upper lip with head held high; see Schneider (1930) for initial description of term, and Estes (1972) for probable olfactory function] provided some indication of impending estrus, as did tail muscle contractions, tail swishing, head tossing, and the intermittent passing of brown (sometimes gelatinous) material in the urine (Fig. 1). Flehmen was observed on 27 different days over the 80-day period from introduction to conception, and on 8 out of 14 occurrences in which the source of the odor could be discerned, "*Rajkumari*" tested her own urine. She also performed Flehmen on 2 out of 10 occasions when she was observed to smell the ♂'s genitalia. However, as already stated, neither Flehmen or any of the other behavioral activities mentioned here could be relied upon to pinpoint estrus.

An exceptionally prolonged period of intense, continuous pacing began at dusk on 23. 9. (one week before the conception) and lasted for 16.8 hours. "*Rajkumari*" walked back and forth along the bars of the cage or along a wall, she frequently went outside and walked around the enclosure, and she curtailed her contacts with the ♂. The temperature of the surface of her body rose perceptibly; her skin was very warm to the touch. After lying down for 5.6 hours during the afternoon of 24. 9., pacing was resumed at dusk and continued until 08.32 hours the next day. Her skin temperature remained abnormally high. Another long spell of lying down followed, and only three 5—10 minute periods of pacing occurred the evening of 25. 9. The ♀ entered the water tank at 20.15 for a stay of 4.5 hours. No observations were made from 01.00 to 06.00 on 26. 9., but the surface of the ♀'s body was still warm at 06.00, suggesting that "*Rajkumari*" could have been pacing between 01.00 and 06.00. Pacing was steady for 30 minutes between 07.13 and 07.43, but shortly thereafter the animals lay down for a long rest until 13.55; by the evening of 26. 9., the ♀'s skin temperature was essentially normal. In summary, pacing was intense on 23. and 24. 9., a week prior to conception, and continued intermittently and only for short periods ($<$ 1 hr) up to the day of conception.

Pacing was also observed for periods of less than an hour in the early morning on 5 separate days as the ♀ approached her first estrus, including the first day of estrus (12. 8. 1972) and the 2 preceding days (Fig. 1). Although the pacing was not protracted and continuous as in the pacing associated with the onset of the second estrus, it appeared to be a significant sign of restiveness related to impending estrus. This suggestion is supported by the absence of pacing for 41 days after the first estrus. Experienced local field observers informed S. Dillon Ripley (pers. comm., Ripley 1952; Hutchinson and Ripley 1954) that ♀ Indian rhinoceroses wander over great distances (presumably for days) when estrus is imminent.

Behavior of the ♂

The most remarkable behavior of the ♂ was a "dance", which was observed 3 times within a half hour (08.30—09.00), 10 hours prior to the first mount during the ♀'s mid-

August estrus, and once again on 27. 9., 3 days before completed copulation took place (Fig. 2). With rapid, vigorous movements the ♂ ran around the center of his cage in a tight circle. Despite his weight (ca. 2300 kg) and bulk, the ♂ was surprisingly nimble. Several times he gracefully reversed his direction, lifted his forefeet 10—30 cm off the floor and whirled first in one direction and then in the opposite direction; at the same time he repeatedly tossed his head high into the air and urinated in strong, posteriorly directed sprays. The action was fast, impressive to the viewer, and reminiscent of a stallion performing in a circus ring. Each dance began suddenly, and ended abruptly with the ♂ standing quietly for a minute or 2 in his urine-soaked cage. The ♂'s readiness to mate and the imminence of the ♀'s estrus seem to have been heralded by the ♂'s dances.

The intense urination during the dances was all by powerful posterior spraying in bouts of 3—5 squirts. According to keepers, such spraying was "*Tarun's*" normal mode of urination. The penis was almost constantly extruded (ca. 20 cm) from the sheath. When excited, as during the dance or when estrus was impending, urine spraying increased in frequency and forcefulness, at times reaching over a distance of 2—3 m. Almost invariably, passing through a doorway, an open gate in the outside enclosure, or the entrance to the water tank triggered spurts of urine. This was the ♂'s most stereotyped behavior.

Field observations indicate that squirt-urination is performed by only the strongest ♂♂ in a given locality and that ♂♂ who urinate in this fashion are usually victorious in agonistic encounters with ♂♂ who do not squirt-urinate. Individual ♂♂ may squirt-urinate for several months and then cease to show this behavior for long periods; however, the individual ♂♂ in a given locality are not synchronous (Laurie 1975). Laurie believes this may indicate that individual ♂♂ periodically come in and out of breeding condition although wild populations as a whole show no breeding seasonality.

Long, steady urinations were seen only occasionally, and then mainly preceding defecation. On the morning of 13. 8., after attempting to mate all night, the ♂ had a prolonged urination, punctuated by many strong pulsations, as he stood facing the ♀. Two other observed long urinations in July were without pulsations and were followed by defecation; 4 observed after the incomplete mating were all characterized by pulsations and were not followed by defecation.

Flehmen as a process in testing the ♀'s urine, presumably in relationship to her receptibility to mate, was observed almost daily (Fig. 2). As "*Rajkumari's*" estrus approached, "*Tarun*" did perform Flehmen more frequently and intensely; increasingly he licked urine on the floor (ingesting the brown gelatinous substance when available), lapped urine from the drainage trough, and ate hay soaked by the ♀'s urine. Ingestion of the urine seemed to have a stimulatory effect on the ♂'s libido. Flehmen was observed immediately prior to the first mount of 12. 8. and 5 times the following day between 09.00 and 15.00, as the interest in mating waned. Over the next 2 weeks Flehmen was greatly reduced, and with the onset of the second estrus, the process again increased in frequency. Flehmen simultaneously with strong squirts of urine characterized the ♂ as the ♀ approached estrus.

The ♂'s libido appeared to be reflected in the frequency of full erections (penis directed forward and tightly appressed to the ventrum) when standing alone, often on rising at daybreak. With the onset of the second estrus, erections were more frequent than before the first estrus (Fig. 2). On 23. 9. the ♂ was filmed masturbating which included pelvic movements, erected tail, and one ejaculation.

During most of the full erections observed, the ♂'s testes were descended into the scrotum. Descent and retraction of the testes could occur within a few seconds and seemed to be under the ♂'s control; testes ascent and descent did not correlate clearly with the ♂'s libido, interactions with the ♀, or the ambient temperature.

Two other aspects of the ♂'s behavior deserve note. The ♂ was seen to drag his hind feet on the morning of 23. 9., the same day he masturbated, and the same day the ♀ began pacing. Foot-dragging was observed also on 24., 25., and 29. 9. before the copulation. Foot dragging has also been observed in the field (Laurie 1974). It often occurs in temporal association with squirt-urination and is also performed by only the strongest ♂♂ in a given locality. The urine provides an olfactory sign of the presence of a strong ♂; while the furrows formed by foot-dragging provide a similar visual sign.

In the 5 years prior to "*Tarun's*" first successful copulation, he had often reacted strongly to the estrous periods of a neighboring black rhinoceros, *Diceros bicornis* L., by banging the walls of the cage, running up and down the fence, and even trying to climb the divider fence. "*Rajkumari*" was ignored during such periods of excitement.

Contact-promoting interactions

The interactions between "*Rajkumari*" and "*Tarun*" over the 80 days of almost continuous access to one another before conception were surprisingly rich and varied. Extremely gentle contact was made at times during mutual horn-rubbing, when nuzzling one another's prehensile upper lips, when the ♀ licked the ♂'s hind leg or genitalia, and when simply lying side by side in a muddy wallow or bathing together in the water tank. On the other hand, violent contact was made during strong head-to-head encounters and when the ♂ initiated wild chases around the outside enclosure by thrusting his horn under the ♀'s flank and attempting to lift her. Usually the ♂ initiated the aggressive interactions; but he also terminated the activity, often exhibiting remarkable restraint. The ♀ promoted most of the gentle interactions by approaching the ♂ while he was lying down or in the pool and engaging in nuzzling, licking, chin-rubbing, backing into the ♂, rump-rubbing or lying down beside him. Similar behavior has been observed both in other captive rhinos (Lang 1961; Schenkel and Lang 1969) and in the wild (Laurie 1973).

Lying together, usually in a muddy wallow, was initiated by the ♀. She approached the ♂ and lay down beside him, often in close body contact (Fig. 3). Usually the ♂ continued lying in the same spot; sometimes he got up and moved off, leaving the ♀ in the wallow.

The ♀ preferred to approach the ♂ while he was lying down or in the pool. Each contact in the water involved the ♀ presenting her rump to the ♂'s face, but once she rubbed her rump against the ♂'s hindquarters. In no case did the ♂ show any perceptible response. "*Rajkumari*" approached "*Tarun*" 28 times while he was lying down, sometimes going to him shortly after an aggressive encounter, whereas she approached him only 7 times while he was standing up. While standing next to the reclining ♂, the ♀ often nuzzled his nose, horn, lips, or the side of his face; backed into him and stood or rubbed her buttocks and genitalia against the ♂'s hind-quarters; rubbed her chin across the ♂'s back; smelled his genitalia; and licked his hind leg and genitalia. Not all of the activities were performed each time.

Licking the hind leg was seen 7 times before the first estrus (Fig. 1), averaging 5.71 minutes in duration (range = 2—12, sd = 3.77); it was noted on 5. and 8. 9. for 15

and 13 minutes, respectively, and for <1 minute on 2 occasions thereafter. During the evening of 29. 7., the ♀ was observed licking the ♂'s genitalia over a 7-minute period, sometimes shifting to the ♂'s side and licking there. On 3 other occasions (<1 min) the proestrus genital licking was extremely brief and seemed inconsequential. The ♂ pulled back and/or lifted his hind leg when the ♀ licked his leg or genitalia. Both the ♂ and ♀ would exhibit a reflexive lifting of the hind leg when the lower leg, inguinal region, or genitalia were stroked or rubbed by a human. The ♂ also would develop a partial erection at such times.

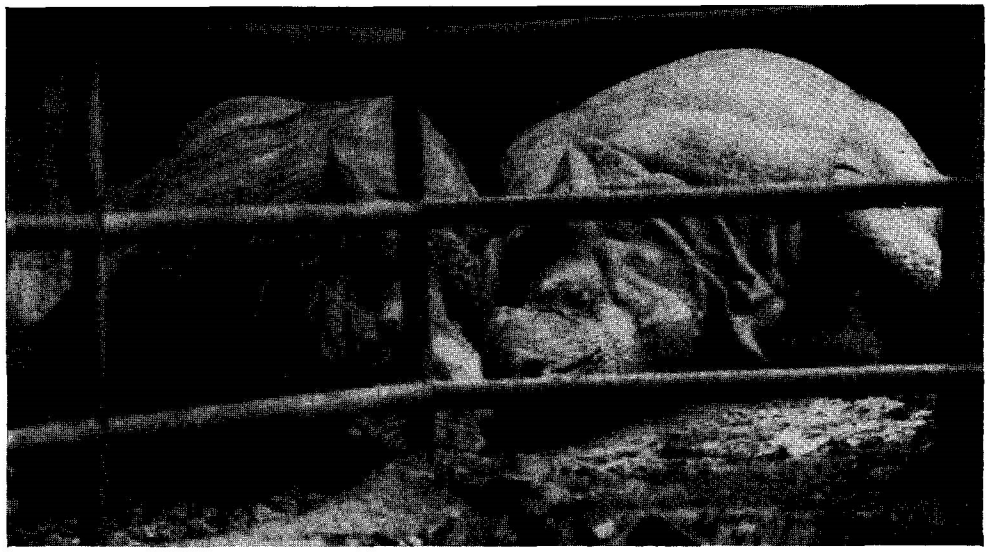

Fig. 3. ♀ (on the right) often lay down beside the ♂ in wallows, apparently to promote contact and arouse the ♂ sexually

Although the ♂ continued lying down when approached by the ♀, he usually responded to the ♀'s active contact (licking, rubbing, backing into him) by standing up within half an hour and often engaged the ♀ in a head-to-head encounter varying from mutual horn-rubbing (Fig. 4) with little or no vocalization to vigorous horn-fighting with vocalizations by the ♀, and openmouth biting directed toward the ♂'s forehead. Occasionally the ♀ inflicted minor wounds on the ♂'s face with her lower incisor tusks. The ♂ kept his head low, seldom opened his mouth or vocalized, and seemed to restrain himself from becoming overly aggressive.

Mutual horn-rubbing was most intense before the first estrus and often lasted 5 to 10 minutes. The rhinos rubbed their horns together gently or with moderate pressure, and often they merely held their horns in contact. Vigorous pushing, knocking, and hard rubbing of the horns occurred before, between, or after bouts of gentle stroking. Before 26. 7., and never thereafter, the ♀ was observed approaching the ♂ on 6 occasions to engage in horn-rubbing; the ♂ approached the ♀ 9 times during the same period of time and 28 times thereafter, often more than once a day, to engage in hornrubbing (Fig. 1 and 2). During the second proestrus the rubbing was both brief and infrequent.

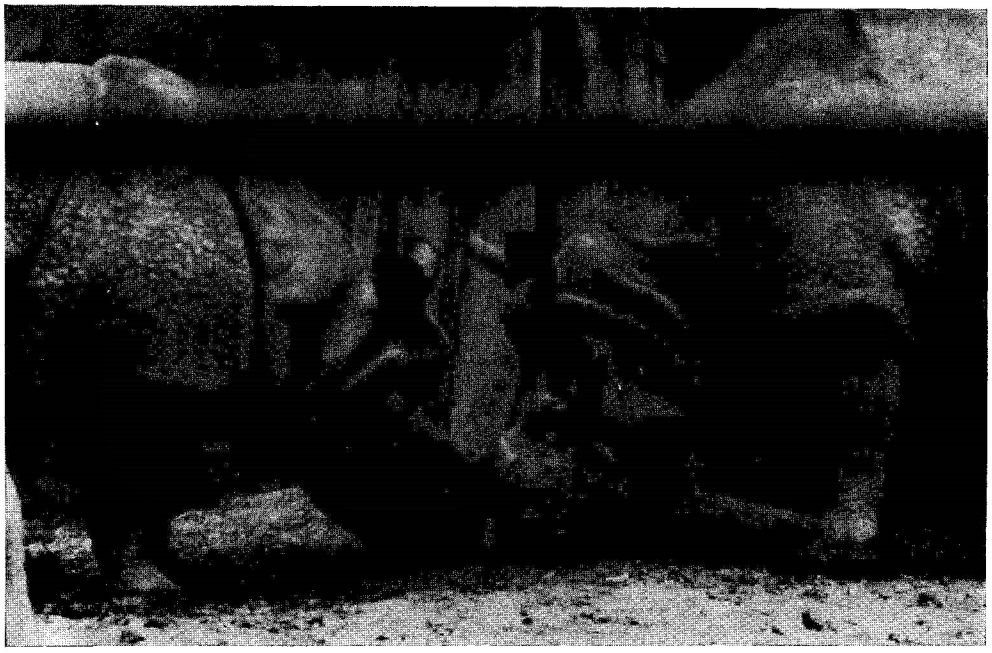

Fig. 4. Mutual horn rubbing, which as usually associated with vigorous head-to-head encounters involving clashing of horns, pushing with horns, open-mouth biting by the ♀, ♀ vocalizations, and other aspects of ritualized "fighting"

Fig. 5. Open-mouth biting by the ♀, which often inflicted minor wounds on the ♂'s forehead when jabbed by the ♀'s lower incisor tusks. Such biting was almost always accompanied by loud honking vocalizations by the ♀, while the ♂ remained silent

Instead of horn rubbing, head-to-head encounters appeared to become more intense and more frequent with the onset of the second estrus, and the ♀ defended her position with greater "confidence" and vigor, threatening the ♂ with open mouth (Fig. 5) loud snorting, and slashing at his forehead with her tusks. Despite the more intense "fighting", however, there were many moments and spells of gentle contact during which the ♀ stroked the ♂'s face lightly with her horn, held her chin on top of his horn, or nuzzled his face with her lip. As with the first estrus, the ♂ approached the ♀ more often with the onset of estrus in late September (Fig. 2).

The most elaborate and interesting courtship activity was observed at night on 24.—25. and 25.—26. 7., the first time the animals were kept together around-the-clock. "*Tarun*" and "*Rajkumari*" approached one another repeatedly and "played" spryly around one of the trees by engaging and breaking horn contact. Nearly always it was the ♂ who broke contact. The ♀ tossed her head, vocalized, and, using the tree as "escape cover", ran from and back to the ♂. When the ♂ lay down, the ♀ went to him immediately and stood over him, rubbed her chin on his rump and back, and backed into him. These initial nocturnal observations suggested the importance of keeping the animals in constant contact.

What appeared to be an "invitation" by the ♀ to the ♂ to chase her was observed 18 times (Fig. 1). On 12 of these occasions, the ♂ and ♀ were in a head-to-head encounter when she broke away, turned, and ran. On 5 occasions, the ♀ tossed her head high into the air before turning and running. Strangely, the ♂ responded to the invitation only twice, and then merely walked slowly toward the ♀. None of the invitations to chase occurred during the week preceding either the first or second period of estrus. The most noteworthy invitation was observed on 23. 7. at 20.09: the ♀ backed up after about 5 minutes of head-to-head encounter with horn-rubbing and pushing, lunged at the ♂, snorted and tossed her head, lunged at the ♂ again, raised her head and twirled her body in a circle and returned to horn contact with the ♂, tossed her head with a circular motion, and galloped away from the ♂. For about 4 minutes she ran around the bathing pool alternately with running up and down the center of the enclosure from the building to the moat; she passed the ♂ repeatedly, snorting at him as she went by. Other than standing and watching, the ♂ did not respond to the ♀'s extraordinary behavior.

During the 80-day observation period, the ♂ chased the ♀ vigorously around the outside enclosure on 8 separate occasions, usually for 4—5 laps. All but one of these chases were both initiated and terminated by the ♂; the exception was on 23. 9. when the ♀ broke and ran after the ♂ who had rubbed her buttocks with his chin for about 5 minutes and then made an intention movement to mount. The ♂ roared, bellowed loudly, and whistled several times as he chased the ♀. The ♀ never chased the ♂.

Except for 2 occasions at the start of a chase when the ♂ attempted to lift the ♀ with his horn in the inguinal region while she was in a corner of the inside cage, and she slipped in struggling to extricate herself, there was no danger of serious injury to the ♀ before or during the chases. Independently of chases, "*Tarun*" occasionally exhibited violent aggressive behavior by roaring, whistling, bellowing, banging the wall, and scraping his face against the wall or steel door — and at the same time urinating profusely (Fig. 2).

In summary, "*Rajkumari*" and "*Tarun*" interacted in a wide variety of behavioral activities at various times through the day. The ♀ made most of the advances during each of the proestrous periods and the ♂ began to take the initiative more often as "*Raj-*

kumari" approached estrus. Seemingly, the ♀ played an active role in arousal of the ♂'s libido. "*Tarun*" chased the ♀ when first reintroduced to her, and again on several occasions about one week before each estrus. A lull in the interactions occurred over the 5—6 days preceding each period of mating activity.

Copulatory behavior

Attempted Copulation — An hour and a half before the first mount on 12. 8., the ♂ began following the ♀ as she walked rapidly from him; when she stopped he forced her to turn by walking around her, and when she walked rapidly again the ♂ stayed directly behind her. This was the first "driving" behavior to be observed. At the entrance to the pool, the ♀ hesitated and then galloped into the building. An hour later "*Tarun*" approached the ♀ indoors, met her with horn-horn contact, forced her outside, and pressed her with his horn until she broke contact and turned. As the ♀ stood quietly, the ♂ placed his foreleg against her thigh and at the same time rested his chin on her rump. Then he raised his leg, pressed his carpel joint against the vulva, and rubbed his cheek on her rump. He raised his right leg and placed his foot on "*Rajkumari's*" back; then he placed his left foot on her back and gradually worked both feet forward. Full erection occurred as the ♂ mounted. However, "*Tarun*" was too far forward, and he did not achieve intromission, his penis passing under "*Rajkumari's*" abdomen. The mount lasted about 5 minutes and he ejaculated externally.

♂ Indian rhinos often have difficulties achieving intromission, because the penis is so long and curved that the ♂ must actually draw back after mounting to reach the actual copulatory position (Lang 1975). Providing young and/or inexperienced ♂♂ lengthy periods of access to estrous ♀♀ may help to overcome this problem.

The pattern of behavior over a 20-hour period of attempted mating on 12.—13. 8. is shown in Fig. 6. Nocturnal observations were made with the night-vision image-intensifier scope aided by the light from a single floodlight mounted on the eaves of the building and directed upward. Because of the limited visibility, nocturnal vulval flashing and horizontal urine-squirting may have been missed, and the pattern of these signals in Fig. 6 may not be an accurate reflection of the ♀'s total estrous behavior. Other details recorded in the graph clearly depict the course of events.

During the first 2 mounts, the ♀ stood firmly; on the next 4, she walked out from under the ♂ each time after tolerating mounting for less than 5 minutes. Between mounts the ♂ followed the ♀ around the outside enclosure and through the cages without pursuing her aggressively. When the ♀ began resisting the mounting, the ♂ began driving her aggressively. Often she chose to circle tightly around a stump, which made it difficult for the ♂ to mount or stay mounted. At times the ♂ ran on his hind legs in an effort to keep his forefeet on the ♀ as she circled the stump. Not until $3^1/_2$ hours after the first mount did the ♂ become somewhat rough with the ♀, putting his horn under her flank and trying to lift as he drove her. The first strong head-to-head encounter occurred at 23.10 with the ♀ biting at the ♂'s forehead; but a mount followed immediately, and 5 minutes later both lay together in a muddy wallow for 10 minutes. At 00.15 the ♂ searched in vain for the vagina as the ♀ stood cooperatively for 5 minutes; finally he dismounted while the ♀ stood firm.

On the next mount the ♂ achieved partial intromission for the first time. The ♀ continued to stand quietly on all but 2 of the subsequent mounts. When the ♀ stood well, the ♂ often scraped his chin downward forcefully on her rump, much as he did against

the wall of the cage when "enraged", and rubbed his chin from side to side across the ♀'s back, much as she did at times while standing over the reclining ♂. From 02.36 to 07.40, no mounts occurred although the ♂ made 5 attempts. Neither animal spent much time lying down during this period (Fig. 6).

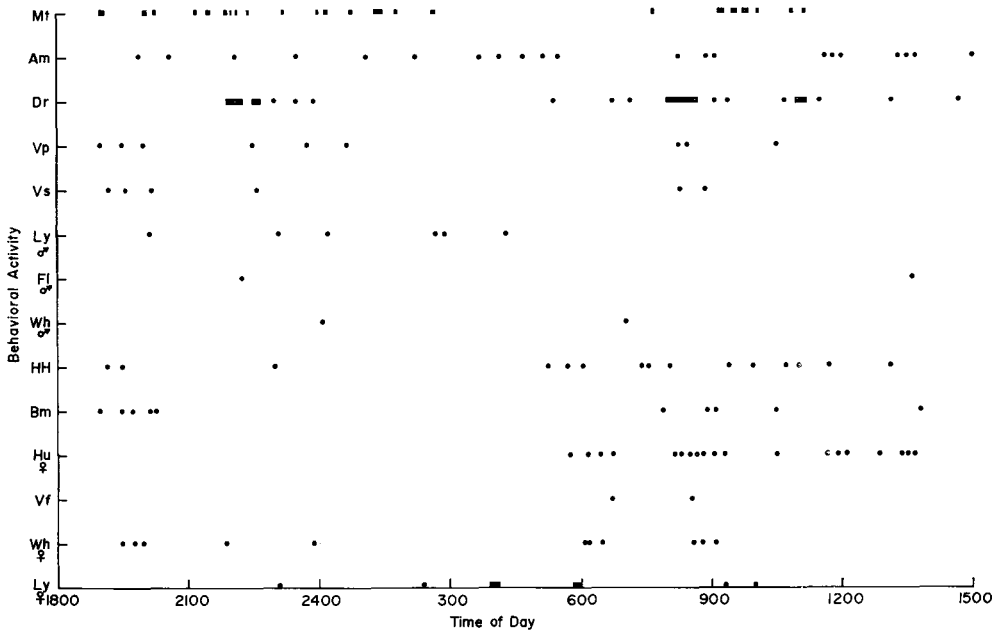

Fig. 6. Behavioral activities of the ♂ and ♀ during 20 hours of mating behavior. Mt = mounting, Am = ♀ approaching ♂, Dr = ♂ driving ♀, Vp = ♂ pressing carpel joint in vaginal area, Vs = ♂ smelling vagina, Ly ♂ = ♂ lying down, Fl = ♂ Flehmen, Wh = ♂ whistling, Hh = head-to-head encounter, Bm = ♀ backing into ♂, Hu ♀ = horizontal urine squirting by ♀, Vf = vulval flashing, Wh ♀ = ♀ whistling, Ly ♀ = ♀ lying down

When the ♀ lay down, the ♂ nudged her strongly in the shoulder, bit her ear, and rubbed her back with his prehensile lip. The ♀ walked, often rapidly, during most of the 5-hour period when she did not allow the ♂ to mount; she appeared uninterested in standing. At 05.40 the pool was refilled and both animals immediately began bathing frequently, but only for short periods (<15 min). The ♂ followed the ♀ in and out of the tank, around the enclosure, into and out of the cages; the ♀ began whistling again with attenuated, high-pitched notes, and frequently urinated in horizontal squirts, occasionally flashing her vulva. At 08.00, the ♂ began to drive the ♀ persistently and an hour later the pair began an intensive effort to mate. With excellent cooperation from the ♀, 6 mounts occurred over a 2-hour period (Fig. 6), but the ♂ never achieved full intromission. Attempted mounts occurred over the next 4 hours, until the animals were separated for feeding at 15.00 hours.

The ♂ continued to be highly animated and aggressive for about 2 hours after the animals were separated; he finally calmed down, fed, and then slept near the ♀ through the night. The animals had free access to one another beginning at about 18.00 hours.

Copulation — Beginning at 03.30 on 30. 9., the ♀ approached and backed into the ♂ several times. From 04.00 onward, the ♂ now motivated, pursued the ♀ persistently. The animals stayed outside in the rain from 05.20 to 05.40, and thereafter walked continuously from cage to cage. The ♂ attempted to mount the ♀ inside the cage at 06.20, and at 06.30 they walked outside where they were not visible for about 5 minutes. Shortly thereafter the ♂ mounted the ♀. The mount was observed from 06.40 to 07.50. The ♂ presumably ejaculated during bouts of pelvic movements which occurred at intervals of 2—5 minutes. The ♀ moved about slowly within an area of about 50 m^2, the ♂ remaining mounted without difficulty. He occasionally relaxed with his head on the ♀'s back, but lifted his head when thrusting.

After the copulation "*Rajkumari*" came directly into her cage, walked around restively, and emitted frequent grunts and soft, high-pitched whistling sounds. "*Tarun*" lay down in a muddy area of the outside enclosure and water vapor rose from his back. When he stood up 45 minutes later, the ♀ approached him, rubbed her side against his hindquarters, and walked back into the building followed by the ♂. Both animals moved in and out of the cages often during the remainder of the day, usually in close contact.

At 07.36 on 1. 10., "*Rajkumari*" walked slowly to the reclining ♂, rubbed her nose against his foreleg, nuzzled and smelled his inguinal region and penis, held her chin over the ♂'s back, rubbed her chin on the ♂'s hind leg, and placed her head deep into the inguinal region. The ♂ stretched out his leg to expose his genitalia. Licking by the ♀ was not discernable. The ♂ dragged his hind feet the morning of 1. 10., had partial erections to ground level, and engaged in gentle head-to-head contacts with the ♀.

Behavior during Pregnancy

"*Rajkumari*" and "*Tarun*" were allowed daytime access to one another daily until 13. 7. 1973, when construction work required their separation. The animals continued to interact during the period of pregnancy. Before conception and for about 3 months thereafter, the ♀ seemed to be subordinate to the ♂. However, as pregnancy progressed, she became increasingly aggressive and defended her cage vigorously, not allowing the ♂ to enter. In the wild, ♂♂ usually flee from ♀♀ with calves (Laurie 1974). The ♂ took his aggression out on the walls of his cage by banging them violently, a habit which gradually decreased in frequency.

Interactions similar to those during courtship occurred during pregnancy and were almost invariably initiated by the ♀. She attempted to engage the ♂ in active contact by tossing her head and running from him (inviting him to chase her), by approaching him from the rear and sometimes rubbing her chin over his rump, and by vocalizing with snorts and honks. During her pregnancy, "*Rajkumari*" exhibited these behaviors fairly consistently during 3 separate periods: October—November 1972, January—February 1973, and June—July 1973. Although the ♂'s response to the ♀'s frequent demonstrations of interest was only occasional, he did respond during each of the periods. The ♀ exhibited signs of interest in the ♂ from mid-October to mid-November, 1972, but was able to elicit a response only on 3 occasions. He chased her on 13. 10., pushed her from behind on 15. 10. and 17. 11., and attempted to mount on 17. 11. "*Rajkumari*" stood during attempted mounting which was little more than an intention movement. The ♂ also responded to the ♀'s sporadic attempts to initiate contact in January and February by attempting to mount on 16. 1. 1973, and by driving her on 2. 2. From mid-June to mid-July, the ♀ approached the ♂ from the rear often, rubbed her chin over

his buttocks on 6 occasions; and invited him to chase once. On 13. 7. 1973 the ♂ responded to an invitation to chase by driving, chasing, and attempting to mount.

During the first part of her pregnancy, "*Rajkumari*" developed a habit of eating feces mainly those of the ♂; this habit peaked within the first 2 months, and had completely tapered off by the 7 month.

Foetal movements were first noted on 19. 11. 1973, 10 weeks before parturition, and a definite enlargement of the udder was observed on 14. 12. at which time the ♀ became increasingly restive and aggressive. She ran to the bars of the cage and snorted when seemingly annoyed by large crowds of visitors and when approached at the bars by keepers and researchers. In late December she was given access to 2 adjacent cages, one covered with canvas to provide privacy. Between the short-lived spasms of irritability and agonistic behavior, "*Rajkumari*" was usually calm; her appetite increased and she slept for long periods. Zoo observers kept watch from 16.00 to 24.00 and from 04.00 to 07.00 between 4. and 30. 1. During these observations "*Rajkumari*" divided her time between the sheltered and open cages, lay down for an hour or 2 at a time, fed often, and became restless whenever the ♂ persistently banged the steel door and wall. As parturition approached, she became more and more intolerant of anyone coming near the cage at any time of day.

Parturition

"*Rajkumari's*" aggressiveness toward keepers appeared to reach a peak on the afternoon of 29. 1. 1974 and a continuous watch was begun at 16.30. Throughout the night she paced back and forth along the walls and bars of her cages, lying down often for less than 10 minutes. While pacing she vocalized almost continuously; and starting at midnight she whistled often (53 times) until 07.00, mostly a brief attenuation of her full one-toned whistle. Her pattern reversed itself at daybreak of 30. 1. and she spent most of the time lying down, rising frequently and walking for brief periods of less than 10 minutes. Her udder and vulva were enlarged and red. The following sequence of events occurred:

07.00 — First slight drainage of urine.
08.40 — Several long periods of fluid elimination began; fluid amber in color, some clear and yellow; color changed within a given outflow.
13.07 — Fluid passed in horizontal bursts and dribbles, often with contractions and vulval flashing.
13.15 — ♀ began straining hard, lying on her side and pushing with her legs against the floor; respiring heavily.
13.20 — ♀ rolled almost onto her back, and assisted by the momentum of the roll, she rose to her feet; contractions of vulva followed.
13.27 — Foetal membranes exposed for first time, then alternately exposed and retracted.
13.40 — Straining increased and membranes pushed through vulva.
13.43 — Forefeet within foetal membranes protruded 2—3 cm from vulva. ♀ alternately lay down, strained, and got up and walked slowly during labor.
13.55 — ♀ rose to her feet, strained, and dropped the foetus, leaving the membranes protruding from her vulva.

As soon as the foetus dropped, "*Rajkumari*" whirled around and touched the calf, "*Patrick*", with her nose, emitted several abbreviated soft whistles, licked the calf, exhibited Flehmen, and intermittently nibbled and licked his hind feet. "*Patrick's*" eyes opened immediately at birth; by 14.00 he made sucking movements and struggled to

stand. He succeeded in standing 105 minutes later and, when taking his first steps at 15.50, immediately began searching for the ♀'s udder. From a reclining position, "*Rajkumari*" lifted her hind leg and rolled onto her side to expose her udder to the calf. For 80 minutes the calf searched for the udder, alternately dozing, waking, struggling to his feet, and tossing his head. During this time the ♀ tried to orient the calf to her udder by rolling farther onto her side and lifting her leg.

At 17.05 the afterbirth was expelled; the ♀ stood up and began eating it. 15 minutes later "*Patrick*" nibbled along the ♀'s flank and thigh and finally nursed 3 hours and 35 minutes after being born. It seemed easier for him to nurse when the ♀ stood. She lifted her leg to provide easier access to her udder. The calf followed his mother, vocalizing in a squeaky bleat, searching, finding and losing the nipple repeatedly. By 18.18 he was fairly well oriented to the location of the udder and had little difficulty nursing thereafter. Throughout the process of parturition and afterwards, "*Rajkumari*" was remarkably calm; all the restiveness and aggression that had developed with the approach of the birth suddenly ceased with the onset of labor.

Postpartum Estrous Cycling

"*Rajkumari's*" periods of estrus occurred at irregular intervals after parturition (Table 1). Dates of estrus were established by the occurrence of vulval flashing, urine squirting and dribbling, and anogenital rubbing. A general increase in alterness, restiveness, inclination to participate in play, and frequency of Flehmen by both the female and the calf seemed to be correlated with estrus.

"*Rajkumari*" exhibited two "strong" estrous periods and several "weak" estrous periods during the 8 months following parturition (Table 1). The first estrous period

Table 1. Evidence of Estrus Subsequent to Parturition

Dates (1974)	Vulval flashing	Horizontal urine squirting	Urine dribbling	Flehmen	Estrous interval (days) ≒
5. 3.				+	34*
6. 3.	+			+	
7. 3.	+	+		+	
8. 3.	+			+	
9. 3.	+				
29. 3.				+	24
31. 3.	+	+	+		
25. 5.			+		57
26. 5.	+		+	+	
28. 5.	+	+		+	
1. 6.	+	+	+		
2. 6.	+	+	+	+	
3. 6.		+		+	
18. 7.	+	+			54
19. 7.	+	+			

≒ Interval between first days of estrous periods.
* Interval between parturition and first estrus.

began 34 days postpartum. The wide variety and 5-day duration of estrous behaviors indicated a strong, clear-cut heat period. Urine-squirting occurred on 7. 3., vulval flashing 6.—9. 3., and anogenital rubbing on 6.—7. 3. An increase in Flehmen was also observed. The strongest indications of estrus occurred from 24. 5. to 3. 6. when vulval flashing, urine squirting and dribbling, and Flehmen were observed nearly every day.

Attempt to rebreed

The ♀ was separated from her calf in the evening and given access to the ♂ for an hour on 1. 6. 1974 and for 30 minutes the evening of the next day. She was extremely aggressive and initiated vigorous encounters with the ♂, charging, butting, biting, and roaring at him. "*Tarun*" usually held his ground, but occasionally ran from the ♀, who chased him around the yard. "*Tarun*" had not been chased by the ♀ previously. The ♀'s strong concern for her "lost" calf, as indicated by pacing restlessly and vocalizing with rapid, successive, abbreviated whistles, alternated with bouts of agonistic behavior toward the ♂. The encounters were significant in demonstrating that "*Rajkumari*" would not accept the ♂ at 4 months postpartum and that breeding at this stage was impossible. In the wild, ♀♀ do not breed again until their calves are about 2 years old (Laurie 1974).

During August the ♂ was put in the outside enclosure adjacent to the ♀ and calf for an hour in the afternoon. This arrangement afforded some visual and olfactory contact between the ♂ and ♀ without necessitating the separation of mother and calf. At first the ♂ was highly excited, climbed on the fence, rubbed his horn vigorously, squirted urine profusely, and ran along the fence. "*Rajkumari*" seemed mildly interested and walked around the yard occasionally, but spent most of her time inside the cage. "*Patrick*" was curious and interested, although frightened at first. He came out only with his mother on the first 3 afternoons and stayed very close to her. Eventually, he ventured outside by himself and even snorted at "*Tarun*". He tossed his head, ran along the fence, and snorted several times, exciting "*Tarun*" who increased urine-squirting and vigorously rubbed against the fence. Occasionally the 3 rhinos smelled each other by getting as close to their respective sides of the wall as possible.

Since "*Rajkumari*" had exhibited her strongest estrous behavior and accepted mounting in August of each year from 1970 through 1972, a period of well-defined signs of estrous behavior was expected in August 1974. Preparations were made to place the animals together at the beginning of the estrous symptoms, rather than late in the period as on 1.—2. 6., with the hope that "*Rajkumari*" would be more receptive to the ♂. However, no periods of overt estrus were evident in August or September 1974, and no endeavor was made to rebreed the animals.[1]

Discussion

It appeared that considerable orientation was required to augment "*Tarun's*" innate reproductive behavior before successful copulation could be accomplished. He may have acquired effective positioning and intromission 2 years earlier than his first copulation had he been given an opportunity to engage in courtship around-the-clock, with

[1] Due to construction, it has not been possible to rebreed the pair to date. We expect to attempt to breed them in the spring and summer of 1977.

free and continuous access to the ♀. Also apparent was an astonishing self-restraint during times of intense aggression. The small size (614 m²) and obstacles (fences, gates, ramps) of the outside enclosure provided an array of hazards that might have led to accidental injury.[2] Yet "*Tarun*" did not seriously injure the ♀ during wild chases, violent horn-to-horn encounters, or while driving the ♀ persistently. Although additional evidence is needed, the observations in this study indicate that considerable manipulation of courtship activity can be accomplished safely to help increase reproductive success of the Indian rhinoceros in captivity.

Prior to his first copulation (at 14 years of age), "*Tarun*" urinated almost exclusively by squirting posteriorly in frequent bouts, and his penis was almost continuously extruded several centimeters from the sheath. After the copulation, horizontal spraying was much reduced, long urinations not coupled with defecation became frequent, and the penis remained inside the sheath most of the time. The frequency and intensity of so called "tantrums" or fits of rage, during which "*Tarun*" pounded and scraped the walls and steel doors, also declined after the copulation, suggesting that "*Tarun*" underwent some important hormonal and behavioral transitions.

The importance of nocturnal activity was well established during the present study. Courtship behavior was especially intense at night when the animals were first placed in continuous contact. The continuous pacing of the ♀ when estrus was imminent occurred almost exclusively at night. Copulatory behavior began at dusk in mid-August and continued throughout the night.

A lull in courtship activity occurred for about a week before each of the 2 estrous periods, comparable to a 4—5 day period of unresponsiveness of a ♂ tiger prior to copulation noted by Kleiman (1974). The observations indicate the importance of maintaining an alert for the time of copulation irrespective of the signs of behavioral estrus.

Indications of estrus were weak during the onset of each of the 2 periods in the summer of 1972. According to Lang's (1961) observations at the Basel Zoo, horizontal urine squirting, vulval flashing, and whistling are particularly reliable indicators of estrus, but all of these signs were weak and erratic in "*Rajkumari's*" case, possibly because she had not yet experienced copulation. After parturition she exhibited 2 strong periods of estrus lasting for about 4 and 7 days.

Vaginal discharge was noted only on the day "*Rajkumari*" accepted mounting by the ♂ and on only one day during the 2 strong postpartum heats. No discharge was observed in the predawn hours on the day of copulation. Seemingly, although the ♀ Indian rhinoceros exhibits signs of estrus over a period of days, she accepts the ♂ only at a peak of readiness, at which time she releases a vaginal discharge. This may indicate that estrus lasts for less than a day, rather than the several days over which signs of estrus may be apparent. Unlike the *Equidae* in which the zebra and horse accept several copulations over an estrous period of 2 to 9 days (Wackernagel 1965; Nishikawa and Hafez 1968), only one copulation occurs at a given estrus in the *Rhinocerotidae* (Lang 1961; Schenkel and Lang 1969).

One of the best predictors of impending copulatory activity was a "dance" by the ♂, performed on the morning of the day mounting began 12. 8. 1972 and again 3 days prior to the copulation on 30. 9. 1972.

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[2] The outside enclosure has now been enlarged to about 1000 m² and redesigned to reduce hazards.

It is noteworthy that, in 23 mounts over a 15-hour period in mid-August 1972, "*Tarun*" achieved intromission only 3 times and then only partially. All mounts were of less than 15 minutes duration, far short of the average of about 60 minutes (Schenkel and Lang 1969) required for complete copulation in the Indian rhinoceros. Resumption of an intense copulatory effort by both animals after a quiescence of about 5 hours (02.36 —07.40) leaves little doubt that artificial termination of copulatory activity is unnecessary because of physical exhaustion. Also there is no evidence for exhaustion of spermatozoa and semen and it therefore seems dubious to terminate copulatory behavior on the basis of physiological exhaustion of the ♂'s reproductive capability. The period of concentrated effort by the ♂ and ♀ on the morning of 13. 8. may have contributed importantly to the successful copulation on 30. 9. 1972.

From the present study the best procedure for achieving reproduction in pubertal captive Indian rhinoceroses is to allow complete freedom of access of the animals to one another at those seasons of the year that are most favorable for breeding. The peak of captive births is in August (Lang 1975), suggesting that the spring months are most favorable for conception. However, our ♀ has consistently shown her most pronounced signs of estrus during the late summer, while the Basel Zoo's ♀ apparently displayed signs of estrus at regular intervals throughout the year (Lang 1961). The possibility that ♂♂ may undergo seasonal changes in reproductive ability (Laurie 1975) introduce a further complicating factor.

Summary

A pair of Indian rhinoceros, *Rhinoceros unicornis*, at the National Zoological Park, Washington, D. C., mated in September 1972 and a ♂ calf was born in January 1974. This paper provides a detailed account of the reproductive behavior which culminated in the successful copulation. These events are of particular interest as both of the animals were sexually inexperienced and required considerable orientation before mating successfully.

The first attempts at breeding the pair failed. We believe that the main factor responsible for the eventual breeding success was that the pair were allowed frequent and prolonged access to each other both before and during the ♀'s period of receptivity.

Most births of Indian rhinos in captivity have occurred during the summer, suggesting that the spring months are most favorable for conception. However, our ♀ has consistently shown her most pronounced signs of estrus during August.

Zusammenfassung

Ein Paar Panzernashörner des National Zoological Park Washington kopulierte im September 1972, und im Januar 1974 wurde ein ♂ Kalb geboren. Die Arbeit beschäftigt sich im einzelnen mit dem Fortpflanzungsverhalten beider Eltern, das in der erfolgreichen Paarung gipfelte. Von besonderem Interesse ist dabei, daß es sich um sexuell unerfahrene Tiere handelte, die vor der gelungenen Kohabitation eines ausgeprägten „Orientierungsverhaltens" bedurften. — Die ersten Verpaarungsversuche waren fehlgeschlagen. Als Hauptfaktor für den endlichen Erfolg wird der Umstand betrachtet, daß das Paar die Möglichkeit erhielt, für längere Zeit, und zwar sowohl vor als auch während der Rezeptivitätsperiode des ♀, beisammen zu sein. Die meisten Gefangenschaftsgeburten von Panzernashörnern erfolgen im Sommer, was den Schluß zuläßt, daß die Frühjahrsmonate am konzeptionsgünstigsten sind. Das Washingtoner ♀ zeigte jedoch im August die ausgeprägtesten Östrus-Anzeichen.

Résumé

Un couple de Rhinocéros Unicornes des Indes du Zoo National de Washington a copulé en septembre 1972 et en janvier naissait un produit du sexe mâle. La publication fait part du comportement de reproduction des parents. Il est intéressant de noter qu'il s'agissait

d'animaux sans expérience sexuelle ayant besoin d'un «comportement d'orientation» très poussé avant la cohabitation couronnée de succès. Les premiers essais de copulation avaient échoué. Comme facteur principal du succès final on considère le fait que le couple avait la possibilité de cohabiter pendant un laps de temps relativement long avant et pendant la période de réceptivité de la ♀. La plupart des naissances chez les Rhinocéros Unicornes des Indes ont lieu en été ce qui fait conclure que ce sont les mois de printemps qui sont les plus favorables à une conception. La ♀ de Washington présentait cependant en août les signes d'oestrus les plus nets.

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