Reproductive Behaviour in Ungulates

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1968

ACADEMIC PRESS

LONDON · NEW YORK

mounting among breeding ewes of the West African dwarf breed of sheep. It is unusual to find examples of male animals which will mount females of species other than their own. Certainly stallions will mount female donkeys and jackasses will mount mares; occasionally sheep and goats will inter-mate (without normal pregnancies occurring, however) but generally the male will only mount a female of his own species.

A recent report by Lehmann (1963) describes three rare instances of abnormal sexual behaviour in farm animals. An oestrous sow was reported to be mounted by a bull and an oestrous mare and an ass were each mounted by heifers. All the animals involved were stated to be accustomed to each other from early life.

"False" mounting attempts are commonly seen in male ungulates. In these the animal mounts apparently normally but quickly dismounts without showing any fore-limb clasping or thrusting movements. The occurrence of these false mounts is circumstantial evidence in support of Jakway's observation that mounting and intromission are separately controlled activities. False mounts of this nature are the rule in the mating pattern of the stallion. In this animal it is usually found that some false mounting will precede an effective one.

Wierzbowski (1959) has made a detailed study of mounting behaviour in the stallion. He found that older animals mounted quicker than young ones, that blindfolded subjects mounted quicker than others and that 2·2–1·4 false mounts seemed to be usual before intromission and ejaculation were effected. In the stallions which were blindfolded it was observed that mounting was undertaken after the male had shouldered the female. The mounting behaviour of the stallion when presented with a dummy mare was also studied and it was noted by Wierzbowski that young, inexperienced stallions mounted the dummy more readily when they were blindfolded than when they could see but still more mounted the dummy when it was visible and sprinkled over with urine from an oestrous mare—all of which points to the positive stimulus of odour and the negative effect which visible features may have on mounting behaviour in this animal. The author has occasionally found that bulls which have a significantly protracted reaction time, and which appear to have their mounting responses inhibited by environmental factors when presented with oestrous cows, sometimes respond to blindfolding by mounting with surprising alacrity.

The oddest of all forms of mounting occurs in the camel. Singh and Prakash (1964) have described the mating behaviour of the camel in India. They record regular grinding of the teeth in the male camel, the

extrusion of its soft palate through the mouth, circling the female, pushing the neck down on to the female's neck and biting the female's shoulder. This behaviour leads the female to assume a seated posture and the male camel then assumes a similar dog-sitting mounted position behind the female. The male extends the forelegs to grip the female and effect intromission. The entire copulation process is reported to take about 15 min.

The report by Backhaus (1958) includes details of mounting behaviour among certain antelope. He describes a very unusual form of mounting behaviour in hartebeest and in the greater kudu. In mounting, the males of these species rise to a fully upright stance on the hind feet before descending on the back of the female. The gerenuk (*Litocranius walleri*) male mounts the female at the walk during which he follows the female on the hind legs without putting the forelegs down. The waterbuck (*Kobus defassa*) makes numerous false mounts during his mating activities (Fig. 39).

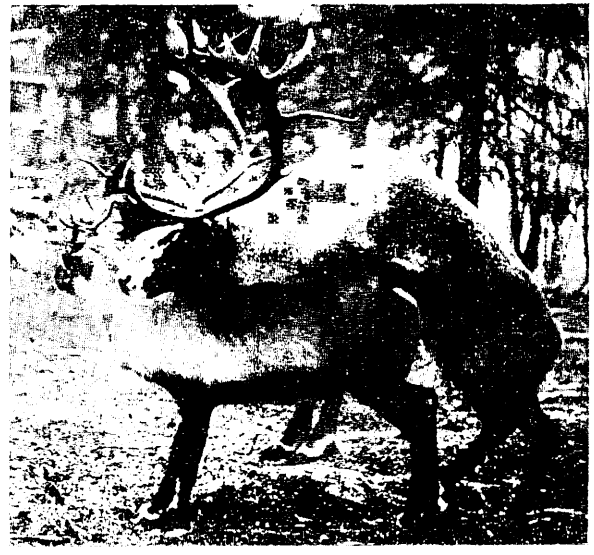

FIG. 39. Copulation posture in reindeer. Mounting and clasping effected but intromission not yet attained. (Photo: Yngve Espmark.)

INTROMISSION AND EJACULATION

Erection of the penis is the physical prerequisite to both actions of intromission and ejaculation. Full erection is normally synchronized

with mounting and thrusting. The mechanisms in the process of penile erection in the bull and ram have recently been re-examined by Watson (1964). He described the process as being one of alternate contraction and relaxation of the ischio-cavenosus muscles under the stimulus of sexual excitement. This localized muscular activity establishes a blood-pumping mechanism which allows the crura to fill on relaxation and empty, with contraction, into vessels of the *corpus cavernosum*. Removal of the sexual stimulus stops the muscular pumping with resultant penile flaccidity. This hypothesis is more tenable than the older one which held that erection was the result of a combination of raised arterial pressure and restricted venous return in the penis.

The erect penis on intromission has increased sensitivity to tactile stimuli and these, in their turn, effect ejaculation. Beach (1952) has demonstrated experimentally that the inadequately developed penis, following castration, has insufficient tactile sensitivity for proper ejaculatory responses to be possible even after the therapeutic administration of significant amounts of testosterone. The early work of Laplaud and Cassou (1945) on electro-ejaculatory procedures showed the role of spinal reflexes in ejaculation. More recently, Russian work has shown that the release of oxytocin, on intromission, contributes to the ejaculatory process in the bull. Bereznev (1963, 1964) demonstrated that significant amounts of oxytocin were present in the bull's blood-stream immediately before and after service. Bulls which were not sexually stimulated or had served more than 5 min previously had no detectable amounts of oxytocin in their blood-stream. At the time of ejaculation there occurs also a peak record of the psycho-galvanic skin reflex (Cordts, 1953) which is indicative of a neural-emotional event analogous to orgasm.

Erection in the stallion is much less rapid than in the bull or in ruminants generally. The muscular type of penis in the horse has a relatively delayed rate of erection. The black rhino bull (*Diceros bicornis*) is reported by Young (1965) as having a delayed and singularly unique manner of penile protrusion and erection. On initial protrusion the penis is bent downwards and backwards and only later does it become straightened and directed forward.

The manner of intromission in the pig is also unique. In this species, the male, when mounted, makes thrusting actions with the penis, which repeatedly makes semi-rotatory actions. Only when the spiral glans penis of the boar becomes lodged tightly in the firm folds of the cervix does this action stop and ejaculation commence. It is clear, in fact, that the locking of the penis in the cervix acts as the essential stimulus to ejaculation in the boar (Fig. 40).

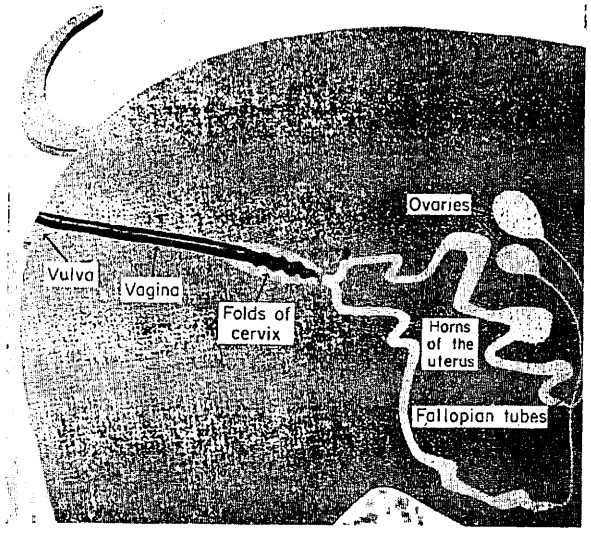

FIG. 40. Diagrammatic illustration of the manner in which the spiral glans penis of the boar becomes locked in the cervix of the sow at mating.

QUANTITATIVE MATING

Following ejaculation almost all subjects have a refractory period. In male animals with full breeding potential this refractory period is usually short. When noting this period in a given individual animal it has to be borne in mind that a co-existing physical disability (e.g. spinal arthritis) can invalidate the observation as an index of innate sex drive. There is abundant evidence to show that refractory periods which become greater after each service with the same female subject do not reflect a physical state of exhaustion but rather a running down in the stimulus value of the female as a sexual object (Almquist *et al.*, 1954). When bulls, for example, are apparently in a state of sexual exhaustion, it has been repeatedly demonstrated that their prompt mating responses are restored when a new stimulus object is presented. Much of this evidence has been discussed previously with particular regard to the bovine subject, but the phenomenon is recognized in other species also, such as the sheep and the pig (Pepelko and Clegg, 1964, 1965a; Jakway and Sumption, 1962).

The number of ejaculations which lead to mating exhaustion varies greatly between species and between individuals. It was reported by Wierzbowski (1964) that stallions, rams and bulls served an average of two, four and eighteen times, respectively, per exhaustion trial. In a

series of depletion tests in stallions, Bielanski and Wierzbowski (1962a) found that the number of ejaculations leading to sexual exhaustion ranged from one to ten with an average of 2·9. The same workers (1962b) reported that the number of ejaculations leading to sexual exhaustion in the jackass varied between one and four.

The boar is capable of a greater number of services before exhaustion occurs. Burger (1952) found that boars in South Africa served oestrous sows up to eleven times in one heat period. Jakway and Sumption (1959) noted similar performances in boars in the U.S.A. where it was observed that each of three boars ejaculated eight times during a 2·25-h test period in which nine oestrous females were available. Berkshire pigs in the Philippines were reported by Quinto (1957) to mate rather less frequently; he estimated that boars mated about five times per heat period in the sow.

The mating performance of male goats was studied quantitatively by Fielden and Barker (1964). They found that eight males which were each subjected to three depletion tests varied in mean number of services leading to exhaustion from four to 12·7. Studies on the service capacities of water-buffaloes in India were carried out by Johari (1960) who found that bulls of this species (*Bubalus bubalis*) gave only one or two ejaculates before exhaustion. This is in very distinct contrast to reports of mating performance in the domestic bull. For example, Almquist and Hale (1956) reported that seventy-five ejaculates were collected from one particular bull in a 5-h period of testing. Mating capacity of a similar order has been reported in roe deer in Scotland by Buxton (1948). He observed a breeding pair walking in a circle for half an hour during which time the buck served the doe on nine occasions.

Some animals with less spectacular mating scores are nevertheless able to carry out large numbers of matings over longer periods of time. The sheep is the best example of this. Hulet *et al.* (1962a, b) estimated that the average ram mated forty-five times in a period of 6 days.

The number of occasions of mating in the female subject is generally low but some variability exists. Hulet *et al.* (1962c) found that ewes were mated six times during the average heat period. Receptivity among ewes is by no means similar however. Lindsay and Robinson (1961a) noted that the oestrual drive varied between ewes and that when only one ram was available, the most active ewes claimed his attention to the exclusion of the least active. A proper proportion of males ensures that all ewes are bred even in large flocks of 6000–7000 (Duran del Campo, 1961). When competition between ewes does occur, it appears that aged ewes are usually more successful than maiden

ewes (Lindsay, 1963). Differences in receptivity in females has also been reported in pigs by Sumption (1961) who found that the more active males dealt effectively with this problem. It was noted that the least receptive females were mated by the sires which had the highest mating frequencies.

A number of reports suggest that matings have the effect of shortening the duration of oestrus in some animals. De Alba *et al.* (1961) gave a convincing account of how the period of oestrual receptivity was shortened by mating in some breeds of cattle but not in others. They reported that the period of receptivity was shortened by as much as 8·7 h in Criollo cattle and 4·1 h in Brahman. They also observed that some cows would permit only one mating per oestrus.

Marion *et al.* (1950) also demonstrated that dairy heifers mated to vasectomized bulls tended to ovulate earlier than those not mated. There is evidence that there is a similar effect in the ewe. McKenzie and Terrill (1937) presented data which suggested that copulation shortened the duration of oestrus in ewes. It may be that a similar event occurs also in the camel. Shalash and Nawito (1964) supplied post-mortem findings which suggested that copulation stimulated ovulation—possibly also accelerating the termination of oestrus.

Pairing

Pairing is most conspicuous in these species which maintain sexual segregation for most of the year, forming intersexual arrangements only during the breeding season. The species which show seasonal breeding, however, mostly have harem breeding systems so that pairing only occurs temporarily in the form of tending bonds which do not persist beyond the restricted oestrous period of the female subject. There are exceptional reports, occasionally, of durable pairings between ungulates. Bourlière (1955) has provided a description of such pairing in the great rhinoceros of India (*Rhinoceros unicornis*). The individuals of this species normally live alone in definite and limited areas during the non-breeding period of the year. In the breeding season they pair and Bourlière describes a case in which one pair were seen to remain exclusively together for 4 months (Figs 41 and 42).

In the much briefer pairing periods of other ungulates a close tending bond is usually evident. In addition, a special positional arrangement has been noted by several observers. The first description of this appears to have been supplied by Schloeth (1961b) who noted the fact that wild Camargue cattle frequently adopted a "parallel and opposite" position during the period when they paired for mating.

The parallel and opposite positioning of the male and the female clearly allows of a most intimate bond between the individuals of opposite sexes when mating activities are in abeyance. By this means, they sustain full lateral contact and association with each other and also are best sited for the mutual receipt of further and continuing

FIG. 41. Nudging in paired rhinoceros. The female is in pro-oestrus.

FIG. 42. Nosing in paired rhinoceros.

pheromonal stimulation. Wohanka (1962), in studying the mating behaviour of cattle at pasture, also noted the adoption of parallel and opposite stances in free mating cattle, as also did Meischner (1963) who not only described this behaviour but gave illustrated accounts of this and other special features of behaviour in paired and mating cattle.

The mating and pairing arrangements in horses have been studied and described by Zeeb (1959, 1961). He noted that before pairing is established mares present their hindquarters to stallions and urinate. After biting by the stallion and kicking by the mare, pairing is often established by nose to nose contact between stallion and mare. During these activities, however, the stallion is constantly providing protection to his entire herd, circling it and examining other females, especially when they respond to his whinnies. Zeeb made the observation that although the qualitative reproductive behaviour of stallions was very similar, there was a great difference between them quantitatively.

IMPOTENCE

Impotence is commonly taken to mean inability of the male animal to copulate. This is a condition which is reported often in domesticated species but rarely in free-living species of ungulates. The extent to which this disorder occurs in wild species remains to be ascertained but undoubtedly it can occur in these animals. There is a well authenticated account of impotence in a king bull in the herd of wild white cattle of Chillingham. The animal had acquired an umbilical hernia, evidently as the result of a fight with a subordinate bull. In consequence of the hindrance of the hernia, although the bull was able to mount his cows, he was unable to effect intromission. This impotence did not prevent the animal maintaining his breeding status which excluded other males from mating activities and the herd entered a period of sterility which was only terminated when the impotent king bull was shot.

Impotence has been fairly well studied in domesticated species because it exists as a factor which adversely affects the economics of animal breeding and because of its fairly common occurrence. Trautwein *et al.* (1958) made observations on 1807 domestic bulls and found that impotence, in the form of disinclination to serve, was the most common impairment of breeding function. Inability to copulate was reported by Hultnas (1953) to be the most common cause of the disposal of bulls in Sweden and Rowson (1946) has also commented on the large number of bulls in England which are discarded because they are reluctant to serve. Rowson discussed the sexual inhibition which appeared to be a major factor in many cases of such impotence and described the somnolent condition in the bull which appears to be prodromal in the development of some cases. The somnolent condition is more widely recognized now and Rowson's opinion of its significance is shared by others. The condition is evidenced by a tendency of the bull to appear somnolent, with its eyes shut, during chin-resting on the