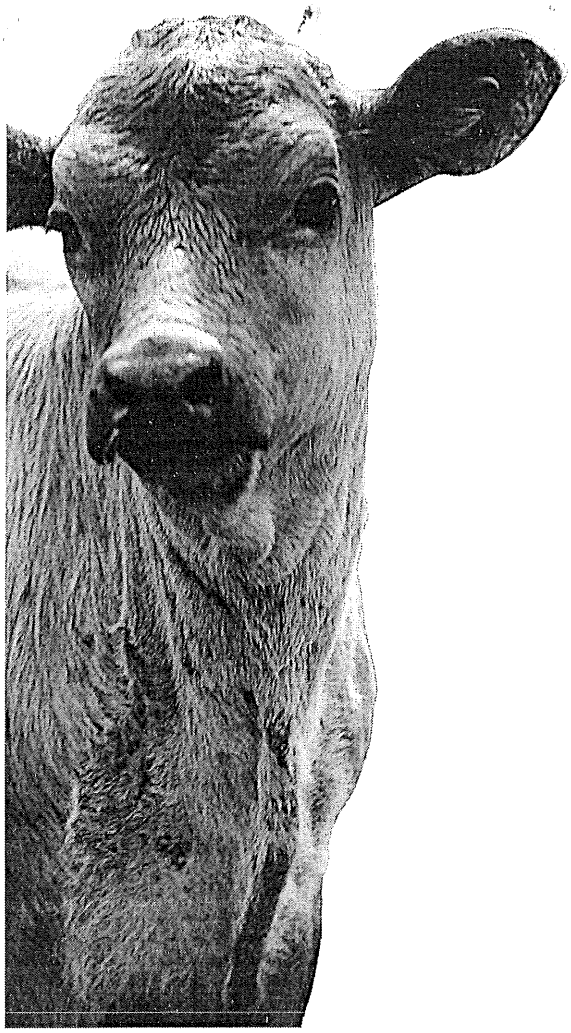
Q103054
ISSN: 0727-6273



A review of beef cattle sexual behaviour, and the factors influencing libido and paternity

February 2003

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MEAT & LIVESTOCK AUSTRALIA

Queensland Government
Department of Primary Industries

QI03054
ISSN 0727-6273

A review of beef cattle sexual behaviour, and the factors influencing libido and paternity

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ABSTRACT

A review of the literature on cattle sexual behaviour was conducted to identify gaps in our knowledge and potential areas for research that may improve the efficiency and efficacy of bull usage in beef cattle herds in northern Australia. This is highly important because natural mating accounts for the vast majority of pregnancies in these herds and there are the economic considerations of the capital costs per calf produced. Furthermore, the genetics imparted by bulls make a much greater contribution to accelerating the genetic improvement of herds than do those of females, and there are major financial gains to be made from using bulls whose progeny have improved growth, fertility, survival, temperament and carcase attributes.

EXECUTIVE SUMMARY

A review of the literature on cattle sexual behaviour was conducted to identify any gaps in our knowledge and whether research was needed in particular areas. More than 100 papers were reviewed, which focussed on the sexual behaviour of bulls and females, the assessment of bull libido (sexual drive or motivation) and the factors that affect the fertility (ability to produce progeny) of individual bulls and of herds.

An obvious feature of the literature is that the majority of the foundation work was conducted in the 1970s and 1980s, and much even pre-dates this. This is not to say that the results from this work are necessarily suspect, but the field of ethology (animal behaviour) has become a much more rigorous scientific discipline in the last decade or so; there has been a move to the testing of specific hypotheses with appropriate experimental design and analyses of data.

It is also noticeable that in previous reviews, references to the same few studies persist and when the original documents were investigated they were frequently found to lack experimental details and robust data. There is, therefore, the potential that many "accepted facts" about aspects of cattle sexual behaviour are far from proven. With these two findings about the literature in mind, it is probably appropriate that some of these areas of research are re-visited.

That said, the review identified some implications for management practices and areas where new research is required.

Implications for management practices:

- sexual activity of bulls can be enhanced or inhibited by the presence of other bulls depending upon their social relationships;
- in multiple-sire mating herds there could be adverse effects on herd fertility if the dominant male is sub- or infertile, as a result of his ability to prevent subordinate bulls from mating;
- in multiple-sire mating herds, bulls that are new to the herd are highly likely to become subordinate and, thus, will sire few calves;
- all bulls to be mated should be introduced to the breeding paddock simultaneously to provide better opportunities for them all to establish territories;
- in multiple-sire mating herds, more equal sexual activity and paternity from individual bulls is likely to be achieved if bull groups are young (less than 3 years), of similar age, genotype and have been reared together; and
- depending upon the way in which they are conducted, serving capacity tests may provide some indication of the libido of bulls to be used in single-sire matings, and they can certainly indicate whether or not a bull is able to mate. However, because of social relationships between bulls, serving capacity tests do not reliably predict the fertility of individual bulls in multiple-sire mating herds.

Questions that require research in order to be answered are:

- Do cattle choose particular mates and what are the bases of mate choice;
- Do cattle prefer to mate with their own breed/genotype;
- What is the role of the female in seeking the bull in dispersed herds;
- Does bull courtship behaviour induce oestrus in females;
- Does pre-mating stimulation of the bull (eg by observing mounting and mating by other bulls) improve sperm quality and fertility;
- Does sperm selection and competition operate in cattle; and
- Does multiple mating with the same and/or different bulls affect oestrus duration and improve or reduce fertility?

Answers to these questions will result in improvements in the efficiency and efficacy of bull usage in beef cattle herds in northern Australia, resulting in major financial gains.

beef cattle sexual behaviour

A review of the factors influencing beef cattle libido and paternity

1. Introduction

This review focuses on the factors that determine whether male and female beef cattle will come together and mate, making the assumption that males and females are physically capable of producing viable sperm and ova, of mating and producing offspring. The review concentrates on the situation of free-ranging cattle, where there is minimal human interference.

In this review, libido refers to sexual motivation, revealed through behaviours such as mate seeking, detection, selection and courtship, and mating and ejaculation. It is not the intention of this review to detail the neurophysiological and neuroendcrinological mechanisms of libido, but rather to review the factors that may affect whether males and females achieve mating and conception. Some factors may, indeed, reduce or eliminate libido, such as may occur when there are other conflicting motivations (eg between libido and fear, or hunger). Other factors may not affect libido *per se*, but rather interfere with and/or prevent its full expression, that is, animals may still be sexually motivated, but circumstances prevent some aspect(s) of sexual activity, such as mating. For example, a bull may be motivated to mate, but the presence of another bull may prevent him from doing so.

The word 'fertility' is widely used in the literature and apparently with various meanings. In this review fertility means the ability to produce progeny.

In the literature the emphasis is very much on male libido, with the behaviour and role of the female being largely ignored. As a consequence of this lack of information on females the emphasis of this review is, also, on the male and, in particular, on factors affecting male libido, as a particular aim of the review is to identify factors that could influence whether particular bulls will achieve paternity. This is important because natural mating accounts for the vast majority of pregnancies in the beef industry and there are the economic considerations of the capital costs per calf produced, which are dependent on the purchase price of the bull, its management costs, the number of calves it produces and its salvage value. Another aspect of the economics relates to the genetics imparted by the bull, which make a much greater contribution to accelerating the genetic improvement of herds than do females, and there are major financial gains from using bulls whose offspring have improved fertility, growth, temperament, survival and carcase attributes.

2. Social organisation

The usual grouping in feral cattle is a matriarchal herd derived from the continued association between mothers and female offspring. The mating system is polygynous, which means that individual males can inseminate many females. Mature males are either solitary or in so-called 'bachelor herds' that join the females only during the breeding season. Where cattle are managed by humans, such social organisations are simulated by 'controlled' breeding (ie the bulls are placed with the females for a limited period of the year). However, in the Chillingham White cattle (a herd of unmanaged, feral cattle in a 134 ha area of parkland in England) males and females are in association at all times and breeding occurs all year. Bulls have home ranges with each home range being shared by two or three bulls. Aggression between bulls that shared a home range is frequent, but rare between those with different home ranges. In these cattle, social behaviour shows seasonal patterns with maintenance behaviours, such as feeding, being the main priority during winter and, as a result, matings are less hotly contested at that time.

Within any group, cattle interact and develop relationships with one another and this leads to the rapid development of what has been termed the 'social order' or 'dominance hierarchy'. This social order remains stable for long periods of time providing that the composition of the group is not changed. In the case of mature animals, the introduction of a stranger will temporarily disrupt the social order until the newcomer establishes itself in the order, but violent fights are rare.

In a wide range of species, the social order is reported to determine order of access to resources and this appears to include sexual access to females by bulls (see section 6.3.2). According to one study, forcing bulls to compete for space in yards produced a similar social order as when the bulls were competing for females during mating in the paddock. In this study, bulls of mixed ages had a more defined social order than a group of 2 year-old bulls. The stability of the social order affected the sexual behaviour of the bulls, and the social order of a group of 2 year-old bulls was more unstable than that of the mixed age group. In the mixed age group there was a significant correlation between the social rank of an individual and sexual activity, with the most dominant animal being most sexually active. This pattern was not seen in the group of 2year-old bulls.

Social rank appears to be determined by the length of time that the bull has been in the herd, and in many cases this was the same as the age of the bull.

However, as will be discussed later in this review, access to females and sexual activity does not necessarily assure paternity.

3. Sexual behaviour

3.1. Seeking and detection by males

Bulls that are not actively seeking-out oestrous cows are unlikely to produce offspring. When no females are in oestrus, bulls spend most of their time on their own resting and grazing, and spend only a small proportion (3.3%) of their time investigating females. It is reported that bulls locate and follow cows for several days before observable (to humans) oestrus. When grouped with oestrous females in a single-sire group, a study showed that bulls spend about 12% of their day in seeking females and in that time walk about 10-12 km/day. The distance declines to about 7 km/day after the first 21 days. In this work no distinction was made between distances moved during mate seeking and those during other activities (eg grazing), but a significant relationship between the distance walked by bulls and the number of females mated has been reported in one study. Other workers have, however, suggested that libido, as measured during serving capacity tests (see section 5.1.1), and locomotory behaviour are unrelated; bulls of high and low serving capacities were fitted with pedometers and grouped, at pasture, with oestrous females. No difference was found between the two serving capacity groups of bulls in the distance that they moved, or in conceptions achieved.

Time spent in seeking and detection could differ with social organisation, as the figures reported above was in a single-sire situation, whereas in a multiple-sire situation it has been reported that bulls may spend about 50% of their time seeking, tending and mating during the first 21 days of joining, with a decline to about a third of their time in these activities in the following 28 days.

Visual and olfactory cues appear to be of greatest importance in the detection of females by bulls, although auditory stimuli are important too. The relative importance of visual or olfactory cues appears to depend on female activity; if there is female-female mounting then bulls will use this as a visual cue for detecting oestrous females, but if mounting is absent then bulls will sniff at the vulva to detect oestrous females.

There is evidence that the perineal skin glands of cows are a source of an oestrous pheromone and the cervico-vaginal mucus from peri-oestrous females contains substances (pheromones) that sexually stimulate bulls. It has been suggested that there may be two pheromones, one for olfaction and that acts as an attractant for the bull, and one for taste or vomeronasal organ sampling that elicits a sexual response. From data obtained during serving capacity tests (see section 5.1.1), it appears that bulls do not use olfactory cues to distinguish between pre- and post-ovulatory females.

The use of different senses is likely to, also, be dependent on paddock size and topography; female-female mounting could only serve as a visual attractant if the bull was able to see the females. Thus, bulls must use other cues (probably auditory stimuli) to initially locate females.

3.2. Seeking and detection by females

Mate seeking is not an activity conducted solely by males; females play an active role and will even solicit attention from a bull by licking, following and mounting him. When in oestrus, cows become hyperactive, with the amount of time spent in eating and resting reduced and the time spent in locomotion, investigation and vocalisation is increased. One study showed that heifers in a single-sire mating system walked about 5 km/day, although it was not possible to determine what proportion of this distance was attributable to mate seeking. The social order (see section 2) between cows is ignored by oestrous cows and, as a result, agonistic interactions become more common. Cow-cow mounting is seen and whilst non-oestrous cows will mount oestrous cows they will not tolerate being mounted. This contrasts with the oestrous cow, which will stand for mounting.

The formation of a sexually active group (SAG) has been described, which comprises oestrous and pro-oestrous females, and appears to serve as a visual attractant to bulls. However, this SAG could only operate to attract bulls if they were in visual contact with it.

Oestrous heifers are reported to spend 97% of their time in the SAG and pro-oestrous animals join and leave it, although spend long periods of time within it for several days before showing signs of oestrus. It is suggested that the females that form the SAG congregate in a small area of the paddock and that the bull or bulls will spend a large proportion of their time with them. However, the SAG is, also, reported to be very mobile, moving, on average, 1 km/h. Most of the time (90%) only a single SAG is formed, but multiple SAGs (two or three) may form, but only when out of sight of each other. As these studies were conducted in small paddocks (2 ha) it is not surprising that single SAGs predominated. However, multiple SAGs would be much more likely in large paddocks with uneven terrain and tree cover, and multiple SAGs would provide the opportunity to allow bulls to form associations with female groups with reduced interaction and competition between the bulls. Indeed, some workers have recommended the use of paddocks with natural barriers to reduce the congregation of bulls at the same group of sexually active females. However, there is little information on the distribution of bulls and females in large paddocks and effects on fertility (see also section 6.1).

Cow-cow mounting was found to be a rare occurrence in a herd of "wild" *Bos taurus* cattle inhabiting parkland in England (the Chillingham White cattle) and it has been suggested that cow-cow mounting is an artefact of cattle husbandry. In this herd, oestrous cows were guarded by a bull against both bulls and cows. Mounting between oestrous and non-oestrous cows was also found to be rare in a group of semi-wild *Bos indicus* cattle because attention from multiple males tended to isolate the oestrous cow from the other cows, although pregnant cows occasionally mounted one another.

3.3. Mate selection

Males and females of any species cooperate in order to reproduce successfully. However, the reproductive strategies of each sex are very different. For the male, the level of investment in reproducing is relatively low compared to the female. The male has only to produce sperm and deposit it in a female in attempting to pass on his genes. In contrast, females have very high levels of investment in their offspring during pregnancy and lactation. For a male, the best strategy is, usually, to attempt to mate with, and fertilise as many females as possible, whereas the female needs to ensure the survival of the offspring. The female's best strategy to achieve this is to ensure high quality offspring. Thus, given the opportunity, females tend to be very selective about their mating partners and try to mate with the best one available.

There is evidence across a range of species (although cattle are not specifically mentioned) that females select good quality males with which to mate on the basis of features such as symmetry and/or secondary sexual characteristics, which are reported as reflecting the quality of that male. For example, to grow and carry horns is energetically expensive. Thus, a bull with very large horns is demonstrating that he is of high quality because he can "afford" to have those horns.

3.3.1. Male

We know next-to-nothing about mate preference and selection in beef cattle. Certainly there are many observations that bulls may preferentially serve one or two females over others. In one study, the range of services given to females was one to 27, although 86% were serviced five times or less and 23.5% were serviced once only. There is apparently, also, variation in the number of bulls mounting (and possibly serving) a particular female in multiple-sire groupings. For example, in one trial, the proportions of heifers marked by one, two, three or four bulls were 27, 39, 28 and 6% respectively. Other workers have observed a large number of matings being directed to a few select females in single-sire situations

when (a) there were few females in oestrus at the time the bull was introduced (b) an inexperienced (young) bull was used at the beginning of the joining period (c) a physically fatigued bull was used towards the end of the joining period or (d) a 'permissive' female was present. It is understandable that situations (a) and (d) would result in preferential mating, but the other situations suggest that inexperienced and/or bulls with low libido may not distribute matings across females. However, we are far from certain as to why such behaviours should occur (see also section 3.5).

Preference for particular females may be related to the stage of oestrus, as in an experiment on serving capacity tests (see section 5.1.1) using peri-oestrous females, those females that had most copulatory responses directed to them were those pre-oestrus rather than post-oestrus. It is possible, also, that a female that has been mated by one bull makes her attractive (perhaps pheromonally-induced) to be served again by different bulls, although this concept has not, apparently, been examined. Such a mechanism would allow the operation of sperm selection and competition (see section 4).

There appears to be some evidence (discussed in section 6.6) that cattle have a preference to mate with members of their own breed, but we do not know how this is modified by rearing experience, or the consequences of the preferred breed being unavailable.

3.3.2. Female

In relation to mating, females have long been deemed to be the passive partner. However, the focus changes markedly with our current knowledge of cryptic female choice and sperm competition. We now understand that females can (and do) control paternity through a number of mechanisms. In relation to mate selection they can do this by: (i) copulating only with a preferred male and (ii) determining whether or not ejaculation occurs. We simply do not know whether beef cattle demonstrate mate preference in these ways, although a situation has been documented where a cow determinedly avoided being separated from a group of cows and a bull by a low-ranking bull.

Further, it is reported that there is large variation between females in the number of services accepted by any one bull; some will allow a bull to serve them once, others will stand for more than 10 services. It has also been suggested by one author that, once mated, a cow will not accept mating from that same bull for some unspecified period of time, but will accept being mated by a different bull. However, other workers have found that more than 70% of females were serviced by more than one bull. We are not at all sure if these behaviours reflect preferences for particular bulls, although there seems to be some evidence that oestrus females may prefer dominant bulls.

One study showed the average number of matings per oestrous female to be 1.73, but it is not clear whether this work was conducted in a single-sire or multiple-sire situation. Another study reported one to four copulations per oestrus within a few hours, but did not specify if this was from the same bull or different ones. Another author reports that four to eight copulations will terminate receptivity, and after serving a particular female a number of times, males seek out new females. This has the obvious advantage that a larger number of receptive females will be found and inseminated.

Whatever the mechanisms, such effects provide an opportunity for different bulls to copulate with the same cow, and for individual cows to mate with a number of bulls, both strategies having obvious consequences for the paternity of the offspring, particularly in view of the potential for sperm competition or cryptic female choice (see section 4).

3.4. Courtship

Once a bull has located a pro-oestrous female he will remain in close proximity to her; an activity referred to as 'guarding' or 'tending'. Both the male and female contribute towards this association. During this

time the bull 'drives' the female in various directions. 'Nudging' is also performed, which appears to stimulate the female to stand stationary and this firm stance reciprocally stimulates the bull. The bull will also place his chin over or on the hindquarters of the female ('chinning'). Chinning, together with attempts at mounting, appears to test the receptivity of the female. One trial found that more guarding and following of oestrous females occurred at night than during the day.

As the female approaches oestrus the bull will sniff and lick the area around the vulva and display the flehmen response, which involves extending the neck, raising the head and curling the upper lip. It is believed that this response draws odours through the vomeronasal organ, allowing the bull to detect specific pheromones that identify the stage of oestrus of the female (see section 3.1).

One author has suggested that the nuzzling, nudging and licking of the female by the bull during courtship ('biostimulation') combined with genital stimulation during intromission, can induce oestrous behaviours in the female and increase pregnancy rates. The bases for this assertion appear to be reports by other authors, and studies on artificial insemination and on dairy cows. There appear to have been no rigorous experiments to test this hypothesis.

During courtship, bulls will perform threat displays, although these may also be performed in the absence of females. The display involves arching of the neck and protrusion of the eyeballs, erection of the hair along the back and turning the shoulder towards the object of threat. Bulls will also indulge in "challenging behaviour" that has three main aspects: roaring, pawing the ground, and horning the ground or other objects. The latter is often performed in a kneeling position. It has been suggested that the bare earth patches and craters that result from pawing and horning are the "claiming of territory" by the bulls.

3.5. Mating

Providing that the female is receptive, courtship will be followed by mating (also referred to as servicing or serving). Immobility is a key characteristic that encourages serving and bulls are primarily attracted to the "inverted-U" shape that resembles the rear of an animal. Hence, the successful use of steers and dummies for semen collection, although it is likely that a certain amount of training and positive reinforcement (ejaculation) encourages the persistence of mounting steers and dummies by bulls. It has been suggested that relative immobility of the female is a greater cue for eliciting mounting by *Bos taurus* bulls than is stage of oestrous cycle of the female, but stage of oestrous cycle may have a greater effect on the sexual response of *Bos indicus* x *Bos taurus* bulls. Such differences have implications for the conduct of serving capacity tests (see section 5.1.1).

Copulation consists of a sequence of events: penile erection and protrusion from the sheath, mounting, intromission, ejaculatory thrust and ejaculation, and dismounting. In mounting, the bull transfers his weight to his hindquarters, raises his front legs and moves forward to straddle the female with his forelegs close to the middle of the female's back. The end of the penis sways to and fro until the glans meets the vulva and then the penis is inserted into the vagina. After further intromission the female's vulvar sphincter contracts around the penis, with the result that the bull's *rectus abdominis* muscle contracts suddenly. The bull's forelegs 'fix' on the female's pelvis (or more anterior) and the bull's pelvic region is rapidly brought into direct apposition to the female's genitalia and maximum intromission, leading to ejaculation, is achieved. The muscular contraction of the *rectus abdominis* muscle is so strong that often the bull's hind legs are drawn off the ground, giving the appearance that the bull is jumping. Intromission is performed quickly, the ejaculatory thrust is forceful with semen ejaculated as a single gush near the *os cervix*. The abdominal muscles then relax and the bull dismounts slowly.

There are contradictory results from studies as to when mounting and mating activity occurs. In one study on *Bos taurus* cattle, it was found to occur throughout daylight hours with peaks between 0600 to 1100h and 1800 to 2100h, with little sexual activity during the hours of darkness. In another study on *Bos taurus* animals, workers found that during daylight, in single-sire mating groups, few matings occurred

between 0700 and 1100h and most were between 1400 to 1900h and in multiple-sire groups, matings were evenly distributed throughout the daylight hours. However, these workers also stated that the bulls were more sexually active at night than during the day, as only 30% of mounting marks could be attributed to observed mounts and matings (those in daylight hours). In other work with *Bos taurus* animals, the peak of mounting activity in both cows and bulls was found to be during the three hours after sunrise and the three hours prior to sunset, with least between 1300 and 1600h. However, these workers conducted only limited observations during darkness.

It is likely that the differences in the patterns of activity between these studies are due to methodological differences in conducting observations, seasonal and thermal effects, although there are reports that *Bos indicus* cattle are 'shy' breeders and, as a result, mate in the hours of darkness. However, as *Bos indicus* cattle are the predominant breed in hotter environments this observation could also result from thermal effects. Furthermore, no difference was found between the sexual activity of *Bos indicus* bulls during serving capacity tests conducted during the daytime and at night.

Copulations are most frequent in the early part of oestrus and become less frequent as oestrus progresses. In serving capacity tests, pre-ovulatory cows elicited more copulatory responses from bulls than did post-ovulatory females. Interestingly, these data contrast with the recommendations for artificial insemination, which state that best results are obtained when insemination is performed at, or near the end of oestrus. The reason given is that ovulation can occur two to 26 hours after the end of oestrus, and presumably this refers to overt, standing oestrus.

It has been suggested that *Bos indicus* bulls are more discriminating with respect to stage of oestrus than are *Bos taurus* bulls, which is reflected in their relative responses to oestrous or non-oestrous females during serving capacity tests (see section 5.1).

As would be expected, mating activity is reported to increase with the number of oestrous females, but also in multiple-sire groupings compared to single-sire. In one study, bulls achieved an average of 55 services (range 14-101) in a 30-hour period. Variability between bulls in number of services in a 19-day pasture situation was reported as being two to 105, thus demonstrating the huge individual variation in libido.

The so-called 'serving capacity' of a bull is regarded as a measure of libido, and is the number of services it achieves in a paddock mating period. Serving capacity can be very variable, for example a range of zero to 15 serves in a 7.5 h period was reported by the worker who developed this concept. Serving capacity actually appears to reflect a combination of libido and mating ability in bulls. Serving capacity is reported to be highly variable between bulls and correlated with the proportion of oestrous females mounted and served, and achievement of first oestrous conception, but not pregnancy rate. However, because of the way in which these data were obtained, serving capacity appears not to be a useful general concept. In the experiment in question, groups of bulls were put with groups of oestrous heifers for a 7.5 h period and the sexual activity recorded. Serving capacity was defined as the number of services a bull completed during the 7.5 h period and within a bull herd the animals were ranked on serving capacity. The upper, middle and lower one thirds were classified as high, medium and low serving capacity bull groups respectively. Serving capacity class was, therefore, a relative classification within herds only and had no meaning across herds. This is evidenced by the data showing that in one herd the high serving capacity bulls averaged 10.5 serves compared to 5.0 in another herd, and the medium serving capacity bulls averaged 4.3 serves in one herd compared to 1.3 in another. Thus, depending upon which herd a bull that achieved four or five serves happened to be in, he could be classed as having a high serving capacity or a medium serving capacity. Thus, the large variation in serves achieved by individuals means that the concept of serving capacity is unhelpful in classifying bulls according to libido. Furthermore, it is obvious that high serving capacity bulls would mount and serve more females than low serving capacity bulls because that was the way in which the classification was defined in the study (ie bulls that did more serving were classed as having a higher serving capacity then those that did less). Females that are not served cannot conceive and, so, it is, also, obvious that,

because of the way in which the classifications were defined, bulls with high serving capacities are much more likely to achieve a greater number of conceptions.

The worker who developed the concept of serving capacity test says that its predictive value is a result of the way in which individual bulls distribute their services during paddock mating ie each bull will distribute its services equally to the oestrous females it serves and, as a consequence, a bull will rarely serve a female more than once. However, this suggestion certainly contradicts the findings of other workers (see section 3.3).

When the data from this study on serving capacity, for the serving classes were compared across herds they showed that, for the high serving capacity bulls, a high proportion of females were served more than once (approximately 47% on average), a lesser proportion for the medium serving capacity bulls (about 21% on average) and none at all for the low bulls. These data appear to indicate that high serving capacity bulls have a greater tendency to service females that have been previously serviced by a different bull, compared to bulls with medium and low serving capacities. This finding raises the possibility that serving capacity tests are measuring "sexual competitiveness" rather than the libido of an individual bull ie that high serving capacity bulls appear to have high libidos as a result of being in a competitive situation with other bulls (see also section 5.1.1). Such a bull in a single-sire mating system may not actually have high libido. This hypothesis certainly warrants further investigation.

Libido would be largely academic if cows had to be served once only to achieve conception. However, it has been suggested that, in the field situation, cows need to mate several times, with one or more bulls, in order to accumulate sufficient semen to have a reasonable chance of conception. Work conducted in the 1950s using artificial insemination apparently shows that repeated inseminations increased pregnancy rates. For artificial insemination it is recommended that semen be placed both in the uterus and cervix, as that placed in the uterus reaches the fertilisation site quickly, whilst that in the cervix survives longer. This dual placement method is said to help overcome the unpredictability of the timing of ovulation.

Some work has demonstrated higher pregnancy rates in females served twice or more (range 55.5% to 68.6%) compared to once only (47.4%). However, other work shows that pregnancy rates of heifers in single-sire mating systems did not differ between those being mated once and those mated multiple times. Given that the assertion that more matings result in increased conceptions is based on limited information and data, it would seem advisable to conduct work to confirm this. Indeed, judging from some results, even if this is the case for individual animals, it appears that herd fertility is unaffected by service activity, regardless of whether it is by the same or different bulls.

It is reported that following ejaculation there is an unspecified period of time during which the bull and cow will not mate again. One worker suggested that this is not a physical effect of 'exhaustion' on the part of the bull, but rather that the female loses her stimulation value for the bull. Another worker stated that it results from the female not accepting another service from the same bull, but that she will accept service from a different bull within minutes of the previous one. However, this same worker, in a previous paper, stated that the cow will stand to be mated by the same bull, but that the bull must encourage the female by vulva-sniffing, courtship and mounting. Given that studies in this area have given apparently conflicting results, and the evident importance of multiple matings for conception and paternity, it would seem appropriate for further work to be conducted.

The social environment can influence mating activity. Sexual activity of bulls is increased if bulls have previously watched other bulls mounting and mating, but sexual activity of individuals can be inhibited by the presence of other bulls. This will be discussed in more detail in section 6.3.2.

4. Sperm selection and competition

Sperm selection can operate through mate selection (see section 3.3) by the female copulating only with a preferred male. The female can then select sperm through a number of mechanism: (i) determining whether ejaculation occurs (ii) ejecting sperm immediately following copulation (iii) timing copulations, in relation to ovulation, with multiple males (iv) selecting sperm within the reproductive tract and (v) post-fertilisation selective resorption or abortion of embryos. Thus, copulation and ejaculation does not necessarily ensure paternity. We do not have the evidence for the operation of such mechanism in cattle, but given that there is evidence for these mechanism in other mammals (including humans), it seems likely that they exist.

Additionally, sperm competition can take place. Sperm competition has been defined as the competition between sperm from different males to fertilise the eggs of a single female, and encompasses both behavioural aspects and the physiological events in the female reproductive tract. In mammals, sperm competition is compressed into the short time around oestrus, as a result of sperm remaining viable in the female reproductive tract for a very short time (usually less than 24h) and females being receptive and able to be fertilised only during the short period of oestrus. Again, we are not certain that sperm competition occurs in cattle, although studies on heterospermic insemination (ie the female receives sperm from more than one male within a short period of time near ovulation) indicate that it probably does (see section 6.6).

A number of features have evolved in species in which sperm competition occurs. These are large testes relative to body size, production of large quantities of sperm and ejaculate containing high proportions of motile sperm. During copulation males deposit a large number of spermatozoa into the female reproductive tract, but only a small proportion is retained in the tract. There is evidence of the female reproductive tract selecting against unfit sperm morphs as the sperm move through the reproductive tract. The first sperm to reach the vicinity of the ova are the ones most likely to fertilise them. Sperm dimensions (particularly, long tails) are important in relation to sperm competition because they determine swimming velocity and may also relate to the distance the sperm must swim. It appears that no morphological changes take place in sperm during their movement through the reproductive tract or capacitation (ie development of the capacity in the female reproductive tract to fertilise ova). However, at the ova (vicinity or surface) sperm undergo a change (the acrosome reaction) that assists with egg penetration. Thus, an assessment of morphology of fresh ejaculate will be indicative of whether or not sperm are of appropriate morphology to attain the vicinity of the ova and penetrate them; a high proportion of normal sperm with long tails may be indicative of a high likelihood of achieving conception. Thus, sperm quality and quantity are likely to be key factors determining the fertility of a bull and, although this review is not intended to cover sperm quality and quantity in any depth, it seems appropriate to cite some work indicating whether there is support for these factors affecting bulls' ability to produce progeny.

4.1. Sperm quality

One study found the proportion of primary sperm defects to have a negative effect on bull fertility in multiple-sire mating groups, but it was the least important factor of those included in the model. In another study that investigated semen quality in four cattle breeds (Angus, Hereford, Brahman and Senepol) the factors affecting conception rate in single-sire herds were percent normal (% normal), proximal droplets, detached heads and semen score (motility plus % normal). In Brahman cattle, after the effect of breeding season length had been removed, the most significant factor on conception was percent-detached heads. In Angus, motility was correlated with all reproductive performance indices (total conception rate, conception in the first 21 days, mean calving date and mean calving date of the first half of the herd to calve). Australian workers have also found motility of sperm and the proportion of normal sperm to be correlated with fertility, although in later work with various cattle genotypes and multiple-sire groupings, sperm motility was related to fertility only in 5/8 Brahman cattle. However, other measures of sperm quality based on spermatozoa morphology (% normal) were important contributors to

fertility in Santa Gertrudis and Brahman bulls.

Studies on heterospermic insemination demonstrated that differences in the proportion of offspring from different bulls, using frozen semen, were found to be correlated with semen laboratory tests for estimating fertility. Semen characteristics correlated with fertility are reported to be motility, the amount of DNA damage and number of heparin binding sites.

4.2. Sperm quantity

The amount of testicular tissue determines the quantity of sperm produced, with relatively large testes producing more sperm on a daily basis. Testes weight and volume are highly correlated with scrotal circumference, thus scrotal circumference is an important measure of the sperm-producing capacity of a bull and it is recorded as part of a bull's fertility assessment. However, the data on the relationship between scrotal size and fertility are equivocal, although some authors specify a minimal size. In one trial, no differences in herd fertility were found when bulls with scrotal circumferences ranging between 28.9 and 44.2 cm were joined with 28 or 29 cows. In other work no correlation was found between scrotal circumference or testes tone and fertility in four genotypes of *Bos indicus* bulls in single-sire mating groups. Other research on multiple-sire mating groups has, also, produced equivocal results. One study showed that scrotal circumference positively influenced bull fertility, but in another, scrotal circumference was not a major contributor to the calf output of individual bulls.

The production of large quantities of sperm does not ensure paternity unless the bull can deliver large quantities of fertile sperm at the right time, although there is evidence from heterospermic insemination studies (see section 6.6) that quantity of sperm is important; changes in the proportions of sperm from different males can overcome inherent advantages in fertility of particular males.

4.3. Timing of mating

In birds the last male to mate is the one most likely to fertilise the next ovum, but there appear no clear order effects in mammals. Rather, the male most likely to fertilise the ovum is the one that times copulation so that the sperm are ready to fertilise when ovulation occurs. In mammals the process of capacitation can take up to 6 hours. The frequency of mating would, thus, influence the chance of mating at the most appropriate time. Studies on a variety of species demonstrate that timing of insemination is critical for paternity, and even appears to over-ride any inherent fertility advantages that individuals may have. There is a paucity of data for cattle, but it is likely that the same mechanisms operate.

Thus, paternity in cattle is likely to be determined by the interaction between mating order, delays between matings, timing of matings in relation to ovulation, and number and duration of matings. Evidently, mate guarding (see section 3.4) could have a considerable effect on the timing of, and delay between matings. Bulls show olfactory investigation of females in the peri-ovulatory period and pheromonal information may tell the bull when is the optimum time to mate. Thus, a bull that is guarding and checking a female may permit other bulls to copulate with the female at times that are not optimal, but may exclude them and ensure that he is the one that mates at the optimum time.

It has also been suggested that 'biostimulation' (see section 3.4) induces oestrous behaviours. Thus, it could be that a combination of guarding and biostimulation allows a bull to time insemination to match ovulation. It would be useful to determine whether bulls in multiple-sire groups that conduct most courtship are also the ones that produce most progeny.

5. Assessment of libido

The intensity or strength of libido is something that is extremely difficult, perhaps even impossible, to assess or measure because libido may remain strong even when its expression is eliminated. For example, if it was possible to collect semen from a bull until it was physically exhausted, it would be the exhaustion that would prevent the expression of sexual behaviour, but libido itself would be unaffected. For this reason it has been suggested that libido is unrelated to the frequency of copulation. Even if libido is, technically, impossible to assess it is still essential for cattle breeding enterprises to have some indication that cattle are likely to mate. Studies indicate that some bulls that are unfit to be used as sires can be identified through physical examination, but others are only detected in tests that require bulls to mount and attempt to mate.

In beef cattle, formal tests for libido tend to be conducted only in males, although females may be tested to check for standing oestrus in some situations (eg for artificial insemination).

5.1. Male

Bull libido tests attempt to measure the sexual responsiveness of bulls to females through measures of the latency for bulls to mount and/or ejaculate, counts of 'interest' (such as sniffing at the vulva, time spent with females) and mounts and serves during a set period of time. The so-called 'serving capacity score' of a bull is generally determined in a yard with a number of restrained non-oestrous, or unrestrained oestrous females and is reported, by the worker who developed the test, to be highly positively correlated with the number of services a bull achieves during paddock mating activity and conception rate.

Tests of libido and/or serving capacity generally take place in situations very different to those under which mating will take place. Tests are generally conducted in pens, yards or lots, usually involve two or more bulls and a small number of females. Thus, the animals are confined in a relatively small area and are unable to avoid particular individuals. The bulls are generally not tested in the same social group as will be used for mating at pasture. In most tests there is no participation from females, as they are frequently restrained and even when unrestrained, confinement in yards means that females are unable to avoid particular individuals.

Additionally, the reliability of yard serving capacity tests in demonstrating the sexual activity of bulls can be heavily influenced by test conditions. Some of these factors are the same as those that affect libido in free-ranging situation (and are discussed in more detail in section 6). Young bulls may need to be given the opportunity to learn how to mount and mate prior to testing in order that their true libido is demonstrated. 'Prestimulation' of bulls, by allowing them to view mounting and mating activity, prior to the test appears to increase libido, as does competition between bulls. However, the number of bulls tested together and the ratio of bulls to females can influence serving capacity as a result of high levels of aggression between bulls, and this appears to vary with different breeds of bull. Whilst non-oestrous, restrained females are generally used in yard tests, these may not be an ideal stimulus for *Bos indicus* bulls, and the use of oestrous, unrestrained females has been recommended for them. However, the use of restrained or unrestrained females may affect the expression of some aspects of sexual behaviour; in one study, more mounts and combined mounts and serves were made when females were restrained than unrestrained, but interest, serves and libido score were not different. It one study it was reported that the use of unrestrained females only discriminated high serving capacity bulls, but the use of restrained females produced a high correlation between pasture and yard serving capacity. If females are restrained, the distance between them can affect the expression of libido by some bulls, as a result of 'interference' between bulls. It has, also, been recommended that test pens be devoid of food that may distract the bulls.

It has been suggested that serving capacity tests should be conducted as follows: bulls should be tested individually to prevent fighting and social inhibition (see section 6.3.2), but placid beef breeds may be tested in groups of three or four, particularly when the groups are of young, same-age males that have been reared together and a ratio of 1:1 is used for males to females. Alternatively, simultaneous individual tests could be conducted, but so that bulls can see each other mounting. Restrained, non-oestrous cows should be used, except with *Bos indicus* bulls, and stanchions should be 8-10 m apart to reduce interference and fighting between bulls. The test pens should contain no food or grass that may distract the bull. The bulls should be prestimulated for 10 minutes prior to testing and young animals may need several tests before their true capacity is expressed.

5.1.1. Libido tests and fertility

A question frequently asked is whether bull libido affects herd fertility. This is not really the question in point, as it is obvious that bulls that are not motivated to seek and mate will never produce offspring. The question that needs to be addressed is "are libido test results related to herd fertility" or, more specifically, "does a libido test result predict the fertility of a bull"?

Given the differences between test and mating situations and the large number of factors that can affect the mating activity of bulls during yard tests it is perhaps not surprising that libido/serving capacity test results do not reliably predict the matings and conceptions achieved by bulls at pasture.

Three studies reported serving capacity score to be positively correlated with conception rate under single-sire mating conditions, whilst another stated that serving capacity score was "useful in assessing bull fertility". One group of workers using multiple-sire mating situations, found that bulls with low serving capacity scores produced fewer progeny than those bulls with medium to high serving capacity scores. However, a number of other authors have reported that the relationship between serving capacity and herd fertility is inconclusive. A large study of different genotypes found that serving capacity score was positively correlated with percentage conception in Brahman herds, and in 2-year old Hereford bulls (but not other ages) and there was no significant relationship in Angus and Senepol herds. Recent Australian work found that there were positive relationships between some measures of sexual behaviour recorded during serving capacity tests, but none were able to consistently predict fertility in multiple-sire mating groups. Other work has been conducted on yearling bulls of high and low serving capacities during single-sire matings. The high serving capacity bulls performed more services, but pregnancy rates were no different between the two treatment groups and the authors tentatively suggested that the effect may have been related to pregnancy rates not differing between heifers being served just once and those being served multiple times. Similar findings were reported by other workers whose study used single and double-sire mating situations. They found that conception rates were no different between high and low serving capacity bulls in single-sire and double-sire situations. Interestingly, these workers found that high serving capacity score bulls performed more services than low in double-sire pasture tests, but there was no difference between the groups in single-sire pasture tests. This perhaps suggests that serving capacity tests may actually measure "sexual competitiveness" rather than libido *per se*.

Other tests of libido have produced similarly inconclusive results. For example, one group of researchers found that high libido bulls (measured as the number of heifers mated by a bull compared to the number in oestrus) did not necessarily achieve high pregnancy rates, apparently due to poor semen quality.

Two studies have demonstrated a low correlation between serving capacity score and pregnancy rate in *Bos indicus* cattle. It is suggested that the reasons for this low correlation is a reluctance of *Bos indicus* bulls to perform sexual behaviour in the presence of humans and, if unrestrained cows that are not fully in oestrus are used, there can be interference from them. Certainly, in a recent Australian study, *Bos indicus* bulls performed fewer sexual behaviours during serving capacity tests compared to *Bos taurus* bulls.

It appears that no single variable can compare libido of individuals, and expression of adult sexual behaviour does not correlate with most of the factors that may be considered to be relevant to producing offspring eg testosterone and luteinizing hormone levels, scrotal circumference, seminal vesicle size, semen characteristics, body size and age at maturity. However, a bull with low libido will produce fewer ejaculates than one with higher libido, although it has been suggested that bulls with excessive libido may rapidly exhaust sperm reserves; in one study, a third of sperm reserves were in the first three ejaculates and ¾ in the first 10 ejaculates into an artificial vagina. Some workers have reported that, in some bulls, excessive mating may be associated with declining fertility as a result of inadequate sperm reserves. This may explain the finding, in one trial, that bulls with moderate to high serving capacity scores produced more progeny than bulls that had very high serving capacity scores.

In conclusion it appears that serving capacity/libido tests will identify bulls that are capable of mating, but they do not necessarily assess libido, because bulls may not express their sexual motivation for a variety of reasons (see also section 6). Further, such tests certainly do not provide a reliable measure of the bull's capacity to produce offspring.

5.2. Female

Female libido is generally assessed through the expression of oestrus. Normally, cycling cows and heifers experience oestrus, on average, every 20 to 21 days and it lasts 13 to 14 hours in situations where females are in association with bulls. There is some evidence that the duration of oestrus may be shorter in cattle kept in tropical conditions compared to temperate ones. One author suggests that breed appears not to influence oestrous duration, but younger animals tend to have a shorter oestrus than older animals. However, a number of other references indicate that duration of oestrus is shorter in *Bos indicus* than *Bos taurus* females.

The period of receptivity is reported to be decreased by as much as 8 hours when repeated matings take place, and behavioural oestrus is reported to be terminated after four to eight services. Further, cows that are grouped with vasectomised 'teaser' bulls have a shorter period of oestrus than those grouped without teasers bulls. Interestingly, one group of researchers reported that heifers grouped with a bull that infrequently completed copulation remained in 'standing oestrus' for a longer duration than did those grouped with bulls that did complete copulations frequently. All of these results suggest that the stimulation of several matings acts to reduce the duration of oestrus. This makes biological sense, as once the cow has received a certain amount of sperm, from one or more bulls, it would be unnecessary for her to continue to remain attractive to bulls, but the suggestion warrants testing.

The intensity of oestrus can be assessed by measures of the amount of soliciting, mounting and standing to be mounted performed by a cow, together with appearance of the vulva and vaginal mucus. The heritability and repeatability of these measures are low and the intensity of oestrus is not directly related to conception. There is also some evidence that sexual behaviour at oestrus differs between *Bos taurus* and *Bos indicus* females; more specifically, the expression of oestrus in *Bos indicus* animals appears less obvious and overt to human observers.

6. Factors affecting libido and conception

6.1. Herd dispersion

The spatial distribution of cattle is likely to restrict the expression of libido, although animals would still be sexually motivated. Thus, the extent to which cattle are dispersed or grouped within a paddock is likely to influence the ease with which bulls and cows are able to locate each other for mating. Indeed, it has been stated that contact between males and females is likely to be less in extensive compared to intensive conditions, but say that this has not been studied adequately. Intuitively this would seem to be the case, as physical barriers, such as steep hills and rivers, may prevent males and females from coming together. One group of workers recommended the use of paddocks with physical barriers as a method for reducing 'overlap' between bulls (multiple bulls associating with the same group of sexually active females) in multiple-sire mating groups. The implication is that physical barriers within a paddock could affect the detection of oestrous females by bulls. These workers found that large groups of sexually active bulls and cows congregated in the paddock and suggested that this resulted in inefficient use of bulls, although there was the advantage that fertile bulls could compensate for any infertile ones.

In a recent northern Australian study, a movement range index (MRI, a measure of a bull's "home range") was calculated for bulls in a multiple-sire herd in a 22 km^2 paddock of open eucalypt savannah woodland, containing numerous gullies, some hills and two main water sources. The researchers found that MRI was unrelated to either social dominance or bull age. However, the bull with the highest MRI sired two to four times the average number of calves sired per bull, and those with the lowest MRI sired no more than half the average. Further, pairs of bulls were frequently found together and in each pairing one bull was considerably higher in the social order than the other and, on average, sired four times the number of calves compared to the subordinate member of the pair. When the proportion of bulls was reduced from 3.7% to 2.8% there was no change in conception pattern, indicating that the fewer bulls were able to locate oestrus cows and impregnate them, apparently by increasing their MRIs. At a proportion of 3.7% the bulls were not evenly distributed throughout the paddock, although the cows were; more bulls were located at one end of the paddock and were found with females on about only half of the observations. In contrast, the bulls at the other end of the paddock were with cows on most observations.

Studies on cattle dispersion are limited; in one study, over a 5-year period, it was reported that a herd of 300 cows divided into sub-groups of less than 80 animals, with the average ranging between four and 11 animals. Another study reported groups of six to 12 animals grazing close together (less than 5 m apart for 50% of grazing observations), with larger groups being formed when resting at camps (20 to 40 head). A number of factors are reported as affecting sub-group size, including the quantity and quality of feed; the weather; location of watering points and the extent to which cattle graze away from them; topography; camping sites; and presence of faeces and urine. It is reported that, in central Australia, cattle densities averaged zero to nine animals/km^2, but following localised rainfall and fresh pasture growth, densities were up to 40 animals/km^2 because cattle home-in on fresh, green growth. It has also been reported that there are "walkers" and "non-walkers" in cattle, with the latter grazing close to watering points. Most cattle graze within 4 km of water and only go beyond this distance if pasture conditions are poor. Other workers have demonstrated how cattle distribution is influenced by the animals' preferences for particular vegetation communities; in one particular study the cattle grazed in grassland and closed heathland, but avoided mossbeds.

6.1.1. Terrain

It has been claimed that double the number of bulls are required to maintain calf numbers when cattle are on rough, rocky rangeland compared to level ground. It is presumed that this is because the bulls have greater difficulty finding the cows. However, this assertion appears to ignore the role of the cows in seeking the bulls and the supporting evidence for the claim was a single report published in 1919, which contains no experimental data.

6.2. Male:female ratios

Libido per se is unlikely to be affected by male:female ratios, but the issue is whether there is a limit to the numbers of females that bulls are able to inseminate with sufficient sperm to achieve conception.

A number of studies illustrate that the ratio of bulls to cows is a critical factor in achieving conception. In one study, when the ratio was 1:20 or 1:30, 95-100% of oestrous cows were mounted, but the proportion declined to about 65% when the ratio was 1:60 and declined further to 51% when it was 1:100. On the other hand, another study demonstrated equally good oestrus detection and pregnancy rates at ratios of 1:25, 1: 44 and 1:60 (excluding two bulls that were unable to complete service) and the researchers suggested that a ratio of 1:25 was inefficient because the full breeding potential of the bull was not used. Another study, also, found no difference in herd fertility when bulls were single-sire mated at ratios ranging from 1:7 to 1:51 and one author has stated that bulls are under-utilised at ratios of 1:20 or 1:30.

A recent Australian study compared conception patterns and rates of females in multiple-sire mating groups with bulls at 6% and 2.5%. Although pregnancy rates were lower in the 2.5% bull herd, conception patterns together with observations on pasture quality and body condition scores of the cattle indicated that the reduced pregnancies were not a result of using smaller numbers of bulls. On another site, these same workers found no effect on conception pattern with a reduction from 3.7% to 2.8% bulls (see section 6.1).

6.3. Social interactions between males

Social interactions can both enhance and inhibit the sexual behaviour of bulls. It is probable that it is mainly the expression of libido that is changed through these interactions. There is a problem with many studies that describe the effects of social dominance because most do not explain the method by which dominance was determined. Even when the method is given, details are inadequate to determine if appropriate techniques were used. For example, in one experiment, the so-called "competitive order" of bulls when access to water was restricted was measured, but it's not clear how this method provided information about the social relationships between the bulls. The method appears to indicate that a group of six to eight bulls were observed for 20 minutes, which would appear inadequate to determine all of the relationships. No mention is made of how interactions were scored and how animals that did not interact were ranked. It is of little wonder, therefore, that the authors concluded that the relationship between sexual activity and social rank was unclear.

A method has been described of forcing bulls to compete for space in a yards that produced a similar social order as when the bulls were competing for females during mating in the paddock. In this work, bulls of mixed ages had a more defined social order than a group of 2 year-old bulls. The stability of the social order affected the sexual behaviour of the bulls, with the social order of a group of 2 year-old bulls being more unstable than that of a mixed age group.

It must, also, be remembered that the dominance hierarchy determined in a test situation may not necessarily be the same as that in the paddock mating situation. Factors, such as injuries to, and maturing of bulls act to change the social order.

6.3.1. Sexual activity of individuals

There are a number of reports that the sexual activity of bulls is enhanced by the presence of other males. This pre-coital stimulation of bulls (eg through visual, olfactory and auditory cues associated with sexual activity) is said to improve fertility, with greatest improvement in those bulls with the lowest sperm output prior to stimulation. One author cites evidence that pre-coital stimulation influences sperm motility,

survival rate and conception rate, but the studies cited appear to be mainly in dairy bulls and/or work done in the 1950s. It would be useful to determine whether these findings are applicable to beef bulls and using current technology for semen collection and examination.

One study reported that high serving capacity bulls performed more serves in the presence of another bull, but low did not, which may indicate that high serving capacity bulls express heightened libido in response to mounting activity, or that the presence of another male stimulates them more (see section 5.1.1). Whatever, more sexual activity per bull would be expected in multiple-male situations, regardless of the serving capacity of the bulls.

There are also many reports that the presence of a more dominant male (see also section 6.3.2) can inhibit and/or interfere with the sexual behaviour of others. In one recent experiment the presence (without physical contact) of a 43-month old bull did not affect the sexual behaviour of 15-month old and 27-month old bulls during a yard serving capacity test, although time spent close to the stimulus female was reduced in the 27-month old bulls. When the older bull was physically present he spent all of his time close to the stimulus female and markedly reduced the time that the younger bulls spent close to the female. Thus, the presence of an older, more dominant bull certainly has the potential to restrict access to oestrous females by subordinate males. However, it must be born in mind that, under natural pasture mating conditions, it is unlikely that a single female will be in oestrus at any one time. Therefore, a dominant bull would need to be able to restrict or eliminate access to a number of females in order to prevent subordinate bulls from serving them. There is some evidence that this occurs, although it has, also, been reported that with SAGs containing more than three oestrous females the dominant bull was unable to prevent subordinates serving. However, when there were less than three oestrous females in a SAG the dominant bull disrupted the serving attempts of the subordinates. This disruption by the dominant bull was more successful (87% of occasions) with groups of mixed age bulls than with a group of 2-year old bulls (20% success).

6.3.2. Effects of social dominance order

In one study it was found that bulls in multiple-male mating groups tended to use the same areas of the paddock and the same SAG, and that the number of females mated was affected by the social rank of the bull, with a direct positive relationship between number of females mated and dominance. The researchers found that in multiple-sire mated groups, about 70% of females were mated by more than one bull, but pregnancy rates were no different in multiple-sire and single-sire groups. In another study involving multiple-sire mating of 7 bulls to about 200 cows, 75% of matings observed in the first 21 days of joining were by the dominant (and oldest) three bulls. In the next 28 days, 53% of the matings were to these same bulls. Overall, 67% of the matings were to these bulls, although they checked cows for oestrus much less frequently than the other bulls (355 v 1,050). The subordinate bulls appeared to act as 'oestrus detectors', but they were then displaced by the dominant bulls. The dominant bulls, also, spent more time guarding/tending cows.

It is reported that with a single SAG, the dominant bull spent more time in its proximity (91%) than subordinate bulls (53%). These results contrast with other findings that multiple bulls, regardless of dominance rank, associated with the same SAG. A recent Australian study showed that dominant bulls spent more time with females in one breeding season, but this had not been the case in the previous breeding season. However, in pairs of bulls that consorted, dominance rank was markedly different between pair members, and the dominant bull sired an average of four times the number of calves than the subordinate bull.

One study followed the sexual behaviour of a group of semi-wild cattle in Africa over a 2.5-year period. At the start there were 29 cows, their calves and one adult bull. No cattle were removed and males were not castrated. Young male calves from 4-15 months attempted to mount and copulate, but aggression from the adult bull prevented copulation. However, from 16 months of age onwards the young males achieved copulations. Dominance relationships operated in another group of 'wild' cattle that are not managed by

humans at all, the Chillingham White cattle. Whenever a cow was in oestrus dominance played a role, but only bulls that shared a home range were observed tending an oestrous cow, whilst those from different home ranges were never seen to do so.

When the social order is not clearly defined, as in one study of a group of 2-year old bulls, serving capacity is reported not to be affected by social dominance. In another study, however, libido and social dominance were negatively correlated in yearling bulls. In groups of mixed aged bulls, it has been reported that the dominant bulls achieved more services than subordinates. However, there were no differences between efficiency of oestrus detection or first oestrus conception rate. The differential effects of group composition on mating are likely to result from the fact that the bulls were of a similar, young age and were probably reared together; young age and long-term cohabitation tends to minimise aggression between bulls. Also, dominance tends to be determined by length of time in the herd, which is often the same as the bull's age (see section 2.). These findings could account for some of the inconsistencies in correlations between serving capacity scores and bull fertility. Bulls could be inhibited during serving capacity tests that are conducted using multiple males and females, or if other bulls are held close by for prestimulation. Such inhibition is more likely to occur if a range of ages of bulls is used, rather than if all bulls are of similar age (see also section 6.3.1).

There is some evidence that oestrous females demonstrate a preference for dominant bulls. One study reported that oestrous heifers solicited attention from bulls by following, licking and occasionally mounting them. Eighty-two percent of such activities were directed to the dominant bull. Such behaviour would have obvious consequences for paternity.

In a recent study, dominant bulls sired more calves than subordinates in one breeding season, but not in the previous one. Overall, there was no relationship between dominance status and calf output in 5/8 Brahman bulls. Other workers showed social dominance to be only weakly (but significantly) correlated with fertility in multiple-sire herds. The dominant bull was the most fertile in two of three paddocks, but lower order rankings were not consistent with fertility. However, to assess dominance the behaviour of the mating groups of bulls was recorded in yards for just one hour, which appears an inadequate amount of time to determine all relationships. When same-age bulls are used rather than mixed age, overall conception rate has been found to be higher and it has been suggested that this is because social dominance is not completely expressed in males of approximately equal size and age. Therefore, there would be less competition between males and less potential for inhibition of libido.

Social interactions can result in physical injuries that can evidently affect the mating ability of a bull. The behaviour, at pasture, of groups of bulls of different ages was compared in an experiment. Animals of 2.5 to 3.5 years of age tended to synchronise their activities and their social interactions were mainly 'amicable'. A proportion of the group of 3.5 to 4.5 year old bulls indulged in a lot of aggressive and mounting behaviours, and demonstrated signs of an increasing tendency to become territorial. In contrast, the bulls aged 5.5 to 6.5 years old had well-defined territories and were independent from other group members. The number of social interactions tended to be small and those that did take place were mainly threats and displays. Researchers suggested that these behavioural differences explain why injuries in bulls at pasture increase after about 2.5 yrs of age to a peak at about 4 yrs of age, then decline.

Another study reported that, in a multiple-sire mating herd, the three older, dominant bulls interacted little with each other and with the younger, subordinate bulls. However, the young bulls still attempted to mate in the presence of the older, dominant bulls, which put them at risk of injury from the older, dominant bulls. Overall, one dominant and three subordinate bulls incurred injuries, and it was assumed this was due to social interactions. Another recent experiment found that there was greater attrition of bulls (2 to 2.5 years of age) when a high proportion of bulls (6%) compared to a low proportion (2.5%) was used. The authors presumed that the attrition was due to increased competition and fighting between bulls and gave an anecdotal report of management problems, such as mustering problems and broken fences, with more than 3.5% bulls in paddocks.

6.4. Age of males

Age evidently affects libido; sexual motivation will be reduced or lacking in sexually immature animals. Furthermore, age will be related to many other factors including social dominance, sexual and other experiences, and sperm quality. As described in section 6.3.2, social dominance has the greatest effect on mating success when males of different ages compete for females. Older males are reported as having a greater tendency for locomotor and genital abnormalities. If this is, indeed, the case then there could be dramatic consequences for herd fertility if those older bulls are less able to mate, and, also, prevent younger bulls from doing so.

In one study of tropical bulls, libido score was found to increase with bull age between 16 and 31 months, and another study found that yearling bulls had lower libido scores and performed more mounts than older bulls. In a further experiment, libido scores generally increased with age in young (12-24 months) *Bos taurus* bulls, but not young *Bos indicus* bulls, which displayed lower libido than the *Bos taurus* bulls. In recent work on yard serving capacity tests, *Bos taurus* bulls increased mounts and serves from 4.6 and 0.1 (during a 20 minute test) to 5.4 and 1.9 between 9 and 25 months of age respectively. In this same study, the mean number of mounts increased between 9 and 14 months of age, but declined thereafter, whilst the number of services steadily increased. Recently, it was found that Santa Gertrudis and Belmont Red bulls showed an increase in the number of serves and libido score in serving capacity tests, with increasing age from 2 to 3 years old. However, the numbers of expressions of interest tended to decrease from 2 to 3 years old and the number of mounts decreased from 3 to 4+ years old. All of these results, taken together, suggest that older bulls become more 'efficient' in serving capacity tests by reducing time spent in any detection and courtship. This is probably not an effect of age *per se*, but rather an effect of sexual experience (see section 6.5).

There are contradictory findings as to whether bull age is correlated with the number of calves that a bull sires. In South African studies over a 5-year period, it was reported that the oldest bulls sired 60% or more of calves, compared to 15% by the youngest bull. In another study, bulls of 1, 2 and 3 years of age were grouped with cows under a multiple-sire management system for an average of 46.6 days. The male to female ratios ranged between 1:14 and 1:30. On average the numbers of calves sired were 4.7, 8.2 and 10.5 for bulls of 1 year, 2 years and 3 years of age respectively. In contrast, recent Australian work found that bull age was not a significant contributor to fertility in multiple-sire herds. However, this was probably a result of bull ages differing by only about one year in most cases.

In another study, groups of five bulls were run with cows for a 6-week breeding period at a bull:cow ratio of about 1:25. For the yearling bulls, three groups of five bulls were used, each being run with the cows for one week and rested for two weeks. Another group of mature bulls (one 3-year old and four 2-year olds) were run with a different herd of cows for the six weeks. Whilst there was little difference in the number of calves born to the yearling and mature bull groups there were differences between bulls. Amongst the mature group the 3-year old bull sired about 41% of the calves, whilst the 2-year olds sired between 9% and 20%. In two of three yearling groups one bull sired 44% of the calves and another bull failed to sire any. In the third group there was no difference between the bulls.

No differences in herd fertility were found in an experiment in which bulls ranging in age from 2 to 6 years of age were single-sire mated. However, in a different trial using single-sire mating there was an effect on fertility of age of bull, although the only effect on sexual behaviour was that older bulls were more efficient (less mounts to serves), probably as a result of experience. Pregnancy rates achieved by bulls in three age groups were 30.2% for yearlings, 40.3% for 2-year olds and 50.7% for those 3 years of age and older (up to 7 years old). Studies in northern Australia, using single-sire herds, demonstrated that pregnancy rates were higher when 3-year old bulls were used compared to 2-year old bulls (72.8% and 66.3% respectively).

In studies where differences in fertility were found, numerous other factors were found to change with age, such as bodyweight, sexual behaviour, scrotal circumference and semen quality. Differences in calf output may have operated through improved semen quantity and quality, as well as higher libido and serving efficiency in the older bulls. One study has indicated that semen quality improves with increased age of a bull, with 1-year old animals having more abnormal sperm than animals of 2 years of age and older. However, this same study indicated that libido, as assessed during serving capacity tests, did not differ with age, although 1- and 2-year old animals made more mounts than older bulls. The workers suggested that this was due to the relative inexperience of these bulls.

Age and bodyweight probably interact and together may play a role through social dominance, but in a study that demonstrated that older bulls sired more progeny, the authors simply assumed that 3-year old bulls would be dominant to 2-year olds and they, in turn, would dominate 1-year olds (this was not actually tested). In northern Australian work, a significantly higher pregnancy rate was found in females mated to 3-year old bulls compared to those with 2-year old bulls, but the average liveweight was, also, significantly greater in the 3-year old bulls.

Mating management may impact on whether or not age affects calf output. A group of researchers investigated bull factors affecting conception in single-sire mating systems in 155 herds over an 8-year period. Only amongst Angus herds was there a significant (negative) correlation between bull age and the proportion of cows pregnant. These results are in contrast to those from other studies in which multiple-sire systems were used, although, in the 8-year study, bulls were mostly used only as 2-year olds in all herds.

All of these results taken together indicate that age *per se* (within certain bounds where semen quality is unaffected) is unlikely to be the factor affecting conception, but, rather, that social interaction between bulls of different ages is the underlying cause (see section 6.3.2). This is further supported by work that used a mixed aged bull group (2 x 2-year olds and a 5-year old) compared to groups of 2-year old bulls. No difference was found between the groups in the proportion of first oestrus' detected or first oestrus conception rate. However, second oestrus detection and conception rates were significantly lower in the mixed age groups compared to the 2-year olds. After 6 weeks the groups of 2-year olds had impregnated significantly more of the females (93.8%) than the mixed age group (84.8%). The author suggested that this was a result of the mating loads and disruption of serving by the old bull in the mixed age group leading to poor serving capacities of the mixed age bulls. Initially there was a high mating load (34 females/week) and the old bull was not able to disrupt all servings by younger bulls. Later the mating load dropped to 11 females/week and at this load the old bull was able to disrupt servings of the younger bulls, resulting in lower fertility. If this explanation is correct, then a difference between the groups in the weekly distribution of conceptions would be anticipated (a reduction in the later weeks for the mixed age groups), but there was no evidence of this.

Age may also affect the ability of bulls to achieve conception indirectly through injury, as discussed in section 6.3.2.

In general, the results demonstrate an age effect on fertility in multiple-sire mating groups, but not single-sire ones, and with greater effects with bull groups containing mixed ages. This suggests that the social relationships between the bulls play a key role, with the older bulls dominating the younger and, as a consequence, achieving more copulations and impregnations.

6.5. Sexual experience of males

It has been suggested that the qualitative aspects of male sexual behaviour are resistant to being modified by experience, and sexual behaviour, including performance in serving capacity tests and measures of libido, of bulls appears to be unaffected by limited contact with other bulls and females during rearing. However, there is a report that rearing bull calves with no contact with heifers resulted in

gestations and postpartum anoestrus periods preventing the cows being in oestrus early in the breeding season.

There is evidence that, generally, *Bos taurus* breeds show higher and less variable levels of libido in test settings than *Bos indicus*. In northern Australian studies, Africander bulls and their crosses achieved the highest libido scores, Brahman and Brahman crossbreds the lowest and European genotypes were intermediate. Similarly, increasing Brahman content resulted in lower libido scores in serving capacity tests. It has been suggested that the commonly-used testing procedures for libido testing may disadvantage *Bos indicus* bulls and to improve the performance of such bulls the test requires modification, such as by the use of unrestrained, oestrous females and the avoidance of extraneous distractions.

One author has stated that Zebu/Brahman bulls have low serving capacities even at pasture due to the situation and the presence of humans. However, they can achieve comparable pregnancy rates, although they display less sexual activity. According to this author these types of bull are said to be selective and "shy" breeders with a tendency to only mount females that are in full oestrus, and they generally do not perform well in pen tests to assess libido. However, despite such observations, a comparison of trials in which bulls were mated with oestrus-synchronised females indicates that Bos indicus bulls were as efficient as Bos taurus bulls in detecting, serving and impregnating available females, despite a lower service rate. Certainly it is reported that some Bos indicus bulls will show levels of sexual activity in serving capacity tests comparable to Bos taurus bulls.

A report from the early 1960s is repeatedly referenced in the early literature as demonstrating that bulls of certain breeds do not 'compete' for mating against those of other breeds. In the study, 21 Hereford and 21 Brahman cross bulls were mated with 600 Hereford cows and only 10% of the calves were Hereford x Brahman. However, when only Brahman bulls were mated with Hereford cows similar numbers of calves were produced as when Hereford bulls only were mated with Hereford cows. The assertion, that these results indicate that Brahman bulls will not compete with Hereford bulls, appears incorrect. A more likely explanation for these data is, simply, that Hereford cows have a preference for Hereford bulls as mates (see also section 3.3). Similarly, it has been reported that when Sahiwal bulls were mated with a mixed group of Sahiwal and Shorthorn heifers, the pregnancy rate of the Shorthorns were much lower than would be expected. The researcher had observed that the bulls appeared to spend much greater lengths of time in association with the Sahiwal females compared to the Shorthorn. Similarly, another researcher recorded that when Simmental bulls from Germany were sold to another country to be joined with the native cattle of that country many of the bulls showed no sexual interest in the cows, although the cows mounted each other. He concluded that this was a result of the bulls imprinting on (developing a preference for) their own breed during rearing. Another author states that males prefer to court and mate females of the species with which they are reared, and generally this is their own species.

There are, also, inherent fertility differences between individual bulls. For example, one study showed that, in a multiple-sire mating system, the bulls that were in the top third of the siring order sired 65-100% of the calves. Other work with multiple-sire mating herds, showed that some bulls sired 70% of the calves, whilst others sired just 4%. These inherent differences are also illustrated through studies on heterospermic insemination. These differences appear to operate through differences in the speed with which sperm reach the ova, attach and penetrate the eggs, which may be mediated through the efficiency of capacitation. A number of studies on bulls demonstrate this, and also that the differences between bulls were modified depending on whether semen was fresh or frozen.

Although it is not within the bounds of this review to discuss all reproductive traits in depth, it is worth noting that there is a wealth of literature demonstrating breed differences in reproductive traits, such as sheath measurements, scrotal circumference and semen quality. Such traits are often correlated with fertility and are likely to be confounded with libido effects on fertility.

the bulls in later life having a tendency to prefer to mount other bulls and avoid cows.

The age of bulls, also, appears to affect efficiency of mating (mounts:serves) and probably reflects the lack of sexual experience of yearling bulls. Young beef bulls learn the correct mount orientation through mounting experience. There is evidence that providing sexual experience to bulls increases sexual activity. For example, one trial reported that number of services was higher in 18-month old sexually experienced *Bos taurus* bulls compared to 12-month old virgin bulls. Evidently age and sexual experience were confounded in this study. In another study of the yard serving capacity test, libido scores and number of services increased when 2-year old, virgin Santa Gertrudis bulls were given sexual experience prior to the test.

As stated in section 6.4, there is some evidence that, with increasing age, bulls show less of the preliminary sexual behaviours, such as interest and mounts, but more serves, indicating greater efficiency of mating with age. This improved efficiency is likely to be the result of greater sexual experience. If, with increasing age, bulls have been exposed to increasing numbers of serving capacity tests then this result may due to the bulls learning (becoming trained) to "perform" in a serving capacity setting; the bulls learn that the females are unable to avoid them and so do not spend time in testing their receptivity, but just serve them. On the other hand, if bulls of different ages have experienced similar numbers of serving capacity tests then the findings are likely to have resulted from the sexual experience of the bulls gained at pasture with females. As stated in section 6.3.2, workers found that the younger, subordinate bulls appeared to act as oestrus-detectors and they were then displaced by the dominant bulls, which mated with the females. It appears that these older and more experienced bulls may have a greater ability to determine the 'optimum' time for mating than younger, less experienced bulls, and do not need to spend time and effort determining the receptivity of the females by repeatedly mounting them. If this is, indeed, the case then it would be useful to know the mechanism by which this superior discrimination is achieved.

6.6. Genetics and breeds

It has been suggested that libido is under genetic control and heritable, with the numbers of ejaculations and latency to ejaculate being highly repeatable in individual bulls. According to another author there is evidence of a hereditary basis for mating competence and serving capacity, and breed differences in sexual performance.

Studies from the 1950s appear to demonstrate the large role that genetics play in determining libido; monozygous twin bulls raised on differing nutritional regimes displayed greater similarity within pairs in mating behaviour than between pairs suggesting a strong genetic influence on this trait, and paternal half-siblings of Swedish bulls differed significantly in libido score with greater variation between sire-son groups than within them. Other studies showing that cross-bred bulls generally exhibited higher libido scores in pen-tests than did their parental pure-breds, also indicate that genetic effects influence bull libido.

In one study, differences in libido scores were observed between breeding lines and sires-within-lines in young bulls of British breeds, and in another, sire strongly influenced serving capacity in young Angus bulls. A heritability estimate of 0.59±0.16 was obtained for serving capacity in a study of 157 paternal half-sibling bull groups in Australia, whilst in another Australian study of 251 Santa Gertrudis, 208 Belmont Red and 189 Hereford bulls, significant heritability estimates for mounts of 0.29±0.14 and 0.57±0.25 were found across all breeds and for Santa Gertrudis bulls respectively, but serves were not demonstrated to be heritable.

Some authors have suggested that Zebu bulls are slower in their mounting reaction of oestrous cows compared to *Bos taurus* breeds. Brahman bulls and cows, under single-sire management for a 60-day breeding season failed to achieve conception rates similar to Angus and Hereford herds in one experiment. The authors, however, stated that this was not due to the Brahman bulls, but rather, longer

6.7. Climatic/thermal environment

Extremes of climatic and/or thermal environments probably operate to reduce the expression of libido. For example, during the English winter, maintenance behaviours, such as feeding, were the main priority for the Chillingham White cattle and, as a result, there was less competition for matings at that time.

Bull libido is reported to be reduced at high temperatures and this 'disinterest' appears to be due to discomfort. It has been suggested by one author who reviewed the literature, that, during hot periods, libido is not affected in *Bos indicus* bulls in contrast to *Bos taurus* breeds, but there may be some depression during cold periods.

6.8. Nutrition

Some studies appear to show adverse nutritional effects on bull libido. For example negative relationships between libido and average daily gain and final liveweight have been reported, and the feeding of high levels of concentrate to crossbred bulls and prolonged nursing/suckling in Angus bulls are reported to compromise the normal expression of libido. However, according to a review by another author, nutritional levels appear to have a minimal effect on libido, although if animals are severely underfed fertility may be impaired.

In one experiment the sexual behaviour towards a teaser was tested in twin bulls, one of each pair having been underfed (30% less crude protein in the diet than the recommended amount) for a period of about 3.5 years from 18 months of age. Despite being about 235 kg less in bodyweight than their control brothers, the underfed bulls were more efficient in their sexual behaviour. Latency to mount, the interval from mounting to copulatory thrust, the interval between first and second copulations and the number of mounts per ejaculation were all significantly lower in the underfed bulls. The author suggested that these results may relate to the physical effort and forces involved in bull mounting behaviour. Although semen was collected, no data were given on the effects of underfeeding on semen quality. There is some evidence, however, that excess nutrition may adversely affect sperm reserves and quality.

6.9. Multiple stressors associated with relocation

There is currently little definitive information on the effects of relocation of bulls to 'stressful' environments and the relative contribution of the various stressors (eg climatic, pathogenic, parasitic and nutritional) to changes in bull libido. A large-scale study in the USA investigated the effects when pubertal Hereford bulls from Montana and Nebraska, as well as Brahman bulls from Texas, were relocated to each other's sites of origin. No changes in reproductive parameters were directly attributed to relocation. The Brahman bulls showed seasonal changes in gonadotropin releasing hormone-induced luteinizing hormone and testosterone in both Nebraska and Montana, while the Hereford bulls showed no seasonal variation in these hormones.

6.10. Temperament and novelty

Cattle temperament reflects the animals' fearfulness and ability to cope with stressors, including those associated with change and novelty. Although apparently referring to semen collecting situations, it is reported that some bulls become apprehensive in new situations and their sexual behaviour decreases until they become accustomed to the new surroundings. The authors say that the length of time to adapt to new situations depends upon breed and age of the bull, with younger bulls adapting faster than old ones. This has implications for the management of breeding bulls as changes of property, paddock, handlers and management procedures are highly likely to temporarily affect sexual performance.

7. Implications for management practices

Many of the factors detailed above will have significant effects on the ways in which cattle are managed in order to optimise fertility. Some examples are given below.

7.1. Conduct of serving capacity tests

Whilst the use of multiple bulls may be desirable to increase sexual activity through competition it cannot be guaranteed that some bulls may not be sexually inhibited by the presence of others. Thus, their true libido will not be revealed. Furthermore, as the social dominance hierarchy relates to specific groupings of individuals, it is likely that serving capacity tests will reveal little about the paddock sexual activity of the bulls unless the same social grouping is used in both situations.

The conduct of serving capacity tests in yards restricts or completely prevents any participation from the females and, therefore, may be unrepresentative of what occurs in the paddock situation. We do not know the effect that being tested for serving capacity has on bulls, but if bulls learn that females cannot avoid them in serving capacity tests they may dispense with courtship. If this behaviour is carried over into the paddock context and, as has been suggested, courtship induces oestrus, there could be fertility consequences for bulls that fail to show courtship in the paddock situation. Furthermore, if mate preference is normally demonstrated by cattle, then there is usually no, or very limited opportunity for animals to demonstrate this is during serving capacity tests.

Serving capacity tests may provide some indication of the libido of bulls to be used in single-sire matings, and they can certainly indicate whether or not a bull is able to mate. However, they should not be promoted and used as a method for predicting the fertility of individual bulls.

7.2. Single-sire v multiple-sire groups

Single-sire mating systems overcome the problems associated with social relationships between bulls, and, hence, resolve the issue of the relative proportions of offspring that particular bulls will sire. However, fertility could be drastically affected if, in a single-sire mating system, the bull is sub- or infertile. Even in a multiple-sire system there could be adverse effects on herd fertility if the dominant male is sub- or infertile, as a result of his ability to prevent subordinate bulls from mating.

7.3. Introducing new bulls

When bulls are introduced to new situations there is likely to be a temporary inhibition of libido, simply as a consequence of the change in environment, and regardless of any stressors resulting from relocation. Bull temperament and age are likely to affect the speed with which a bull will adapt to change and, hence, the length of time during which libido will be reduced.

If new bulls are to be put into a multiple-sire mating system then it is likely that the new bull will be the most subordinate of the group, as length of time in the herd (which is often the same as age) is correlated with social dominance. Thus, a new bull will be at the bottom of the social order and is likely to sire few calves. Bulls develop home ranges and territories, so it is inadvisable to introduce a new bull into the breeding paddock, as resident bulls will have their territories established and the new bull will either be excluded, or have to fight resident bulls in order to establish a territory. All bulls to be mated should be introduced to the breeding paddock simultaneously to provide better opportunities for them all to establish territories.

7.4. Composition of bull groups

More equal sexual activity and paternity from individual bulls in multiple-sire mating herds is likely to be achieved if bull groups are young (less than 3 years), of similar age, genotype and have been reared together. There is also likely to be less aggressive interactions between such bulls and, as a result, less injuries.

8. Areas requiring further research

One of the most obvious features of the literature on cattle sexual behaviour is its age; the majority of the foundation work was conducted in the 1970s and 1980s, and much even pre-dates this. This is not to say that the quality of those studies is necessarily suspect, but certainly in the field of ethology, dramatic improvements have taken place in the methods, technology and conduct of studies in the last decade. These improvements are producing higher quality, and more robust data and results.

It is also noticeable in reviewing the literature that references to the same few studies persist in past reviews and when the original documents are investigated there are frequently a lack of experimental details and a paucity of robust data. There is the potential, therefore, that many "accepted facts" about aspects of cattle sexual behaviour are far from proven. It is probably timely to re-examine many aspects of libido to ensure that previous findings from a limited number of studies are, indeed, sound. In addition there are a number of areas that are, apparently, either unexplored or have given rise to equivocal results to date. The following are some examples and the elucidation of these areas has the potential to have significant benefits on the efficiency of bull use and the speed at which herd genetic improvement occurs.

8.1. Mate choice

The apparent preference for 'like breeds' requires more work. If it is, indeed, the case that males and females prefer to mate with their own genotype then bull genotype needs to be carefully considered in light of the female genotype. This is unlikely to be an issue where there is a single bull, but may play a role where there are multiple males of differing genotypes. We do not know what other factors are involved in mate selection and this needs to be researched further. There is evidence in other species that choice is made on gene quality and compatibility between genetics, being revealed through features such as symmetry and secondary sexual characteristics (see section 3.3). We have no idea if such systems operate in cattle. Given that producers attempt to introduce 'superior genetics' and hybrid vigour into their herds by using bulls of genotypes very different to that of the females, there could be significant consequences of mate choice on herd improvement.

8.2. Sperm selection and competition

Even if a bull mates with a cow, paternity is not assured due to sperm selection. Furthermore, in many species where there is mating by multiple males, sperm competition occurs in the female's reproductive tract. As we do not know if sperm selection and competition operate in cattle, these are areas that warrant further research, particularly as this would provide an indication of the relative importance to fertility of mate selection and sperm competition.

8.3. Courtship and the timing of mating

It has been suggested that bull courtship behaviour may actually induce oestrus in females, but there is, to date, little evidence to support this hypothesis. Also, as timing of insemination in relation to oestrus appears to be a crucial factor in males achieving conception, we need to know more about the effects of courtship and guarding by individual bulls in multiple-sire groups and whether these behaviours are related to the number of offspring produced by individual bulls. Furthermore, it appears that older, more experienced bulls may be much more adept at determining the 'optimum' timing of mating. It would be very useful to determine the mechanism by which they do this in order to improve the efficiency of bull use.

8.4. Multiple matings and termination of oestrus

There are equivocal data relating to the effects on fertility of multiple matings with the same and different bulls. Some studies report that females will accept multiple serves from the same bull, others state that females will accept serves from different males, but not repeated serves from the same male. Furthermore, there are differing opinions as to whether multiple matings improve fertility, and there are interesting observations that indicate that multiple matings reduce the length of oestrus or even terminate it. This whole area warrants further investigation given that it has the potential to have very significant effects on fertility.

8.5. Pre-coital stimulation and sperm quality

There appears to be some evidence that pre-coital stimulation of bulls may result in improvements in sperm quality and fertility. However, as this hypothesis and the data on which it is based are rather tenuous, it is an area that warrants further investigation.

8.6. Dispersion

It has been suggested that cattle dispersion (and the factors that contribute to it) will affect the ease with which bulls locate females, and, thus, influence herd fertility. The emphasis in work on libido has been on that of the bull, and the role of the female in seeking the male has been given little attention. Further research is needed in the area of mate-seeking and the effects that cattle dispersion has on this.

8.7. Relocation of bulls

Given the high probability that bulls will continue to be purchased at considerable distances from where they will be used, there is a need to determine the effects of relocation on fertility and the relative contributions of the multiple stressors to any fertility problems.

8.8. Serving capacity tests and sexual competitiveness

Bulls assessed as having high serving capacity scores (in yard tests) appear to demonstrate the same levels of sexual activity, in single-sire mating systems, as those scored as having low serving capacity scores. However, in multiple-sire mating systems, high serving capacity bulls perform greater levels of sexual activity than do low serving capacity bulls. Furthermore, high serving capacity bulls, also, may have a greater tendency to serve females previously served by another bull, compared to lower serving capacity bulls, but this requires confirmation. These various behaviours may be related to the social relationships between bulls, or, alternatively, serving capacity tests may actually be measuring an aspect of sexual competitiveness, rather than libido *per se*. If serving capacity tests are to be continued to be used as a predictor of bull libido then these issues need to be resolved so that tests can be refined to give more meaningful results.

Acknowledgements

Meat and Livestock Australia partially funded the preparation of this review. I am extremely grateful to Dick Holroyd (DPI Rockhampton) for the time he spent helping to identify appropriate references, and reading and commenting on several drafts of this review. My thanks, also, go to Geoff Fordyce (DPI Charters Towers) and Lex Turner (DPI Mutdapilly) for providing feedback on a previous draft.