

final report

Project code: AWW.0187
Prepared by: Dr Scott Norman¹
Mr John Bertram²
Prof Michael McGowan³

¹ Charles Sturt University
² Qld Dept of Primary
Industries and Fisheries
³ University of Queensland

Date published: November 2008

ISBN: 9781741917420

PUBLISHED BY

Meat & Livestock Australia Limited
Locked Bag 991
NORTH SYDNEY NSW 2059

Prevalence of selected abnormalities in polled and horned bulls which affect breeding soundness

Meat & Livestock Australia acknowledges the matching funds provided by the Australian Government to support the research and development detailed in this publication.

This publication is published by Meat & Livestock Australia Limited ABN 39 081 678 364 (MLA). Care is taken to ensure the accuracy of the information contained in this publication. However MLA cannot accept responsibility for the accuracy or completeness of the information or opinions contained in the publication. You should make your own enquiries before making decisions concerning your interests. Reproduction in whole or in part of this publication is prohibited without prior written consent of MLA.

Abstract

The major objective of this project was to evaluate the evidence of reported associations between specific abnormalities affecting bull breeding soundness (preputial prolapse, reduced serving capacity and premature spiral deviation of the penis (PSDP) and the polled condition.

The systematic review of published scientific literature and industry anecdote concluded that factors not likely to be related to the polled condition, such as sheath structure, probably have a greater influence on the occurrence of preputial prolapse than any negative effect of the polled condition. No evidence was found of a relationship between the polled condition and reduced serving capacity or libido.

The systematic review found that PSDP was likely to be heritable, but there was no evidence it was directly associated with the polled condition. Analysis of serving ability/capacity data from bull breeding soundness data bases provided by 3 veterinary practices and 2 beef cattle researchers confirmed previous reports that the prevalence of PSDP increases with age, being markedly greater in bulls ≥ 3 years of age. For bulls ≥ 3 years of age approximately twice as many cases of PSDP were detected in polled-breed bulls (13.5%; n=496) than in horned-breed bulls (5.6%; n=233), clearly indicating that it is a much greater problem in polled-breed bulls but occurs frequently enough in horned-breed bulls to suggest that it is unlikely to be simply associated with the polled gene.

With the likely greater use of polled-breed bulls in beef herds, producers of polled-breed bulls should be encouraged to conduct serving capacity tests on their ≥ 3 -year old herd sires to identify those affected with PSDP. Further, with the support of relevant breed societies and geneticists, strategies which may include the use of DNA marker technology should be established to enable seedstock producers to select against this problem.

Executive Summary

The MLA funded project AHW.094, 'Genetic options to replace dehorning of beef cattle in Australia' found there were potential associations between the polled condition and abnormalities affecting the breeding soundness of bulls. The researcher recommended that these possible associations be further investigated to define the potential magnitude of the problem.

The current project consisted of two parts:

Part 1: A systematic review was conducted of published scientific literature, reports from breed societies in Australia and elsewhere in the world, and unpublished studies and reports from researchers and reproductive specialists on the occurrence of breeding soundness abnormalities in polled and horned bulls. Three conditions affecting bull fertility have been implicated as being associated with the polled condition. These are preputial prolapse, reduced serving capacity, and premature spiral deviation of the penis (PSPD).

Part 2: Retrospective analysis of the findings of serving ability/capacity testing derived from BBSE data bases provided by 3 veterinary practices (north-west and central NSW, southern WA) and 2 beef cattle reproduction researchers (WA and Qld) was conducted to determine the prevalence of PSPD by breed, age and breed-horn status.

Based on the findings of Part 1 the association between preputial prolapse and the polled condition in bulls may be summarised as follows:

1. The polled condition is almost certainly associated with a higher prevalence of reduced size, or absence of the caudal preputial muscle. Reduced, or absent caudal preputial muscles seem to be associated with an increased prevalence of preputial eversion.
2. There is no scientific evidence that an increased prevalence of preputial eversion is related to an increased prevalence of preputial prolapse in *Bos taurus* breeds. However, in some *Bos indicus* derived breeds there is some evidence to suggest that an increased prevalence of preputial eversion may be related to an increased prevalence of preputial prolapse, and the findings from one small study conducted in Queensland suggest that polled bulls may have an increased risk of preputial prolapse compared to horned bulls.
3. Bulls with poor sheath structure and a propensity for preputial eversion may be more at risk of preputial prolapse, and this conformational combination is more likely to occur in *Bos indicus* derived breeds. In contrast, a bull with good sheath structure (as is more likely with *Bos taurus* breeds) and a propensity to evert has minimal risk of preputial prolapse. That is, sheath structure may be the pivotal trait determining the occurrence of preputial prolapse, with reduced function of the caudal preputial muscles and preputial eversion being significant only if associated with poor sheath structure.
4. Dissemination of the poll gene is unlikely to significantly increase the prevalence of this preputial prolapse. Sheath scoring systems are available (Breedplan and Australian Cattle Veterinarians) which could be used to assist producers with the selection of bulls with satisfactory sheath structure. The heritability of sheath structure is considered to be moderate.
5. Further, there appears to be no evidence implicating a relationship between the polled condition and reduced serving capacity or libido, and except for PSPD no other conditions affecting bull fertility that could be directly related to the polled condition were identified.

Breeding Soundness Abnormalities in Polled and Horned Bulls

Based on the findings of Parts 1 and 2 of this project, the association between PSDP and the polled condition in bulls may be summarised as follows:

1. Evidence of the association between these two traits is generally based on anecdote, or studies performed 23 to 50 years ago on relatively small numbers of animals (except one Australian study). Examination of the data in these studies indicates PSDP is more likely to be associated with breed and familial lines, in contrast to a specific association with the polled condition. Subsequent authors referring to these studies have perhaps erroneously concluded that the higher prevalence of PSDP in polled breeds implies a direct association with the poll gene. An Australian study of 1,000 *B. taurus* bulls found that 16% of polled-breed bulls had PSDP compared to 1% in horned-breed bulls.
2. PSDP was by far and away the most common abnormality affecting the serving ability/serving capacity of bulls detected by veterinarians and researchers in Part 2 of the project. It was rarely detected in young bulls (1- to 2-year olds) but across breeds 8.2% (n=939) of 3- to 6-year old and 18.4% (n=179) of >6-year old bulls were diagnosed with PSDP. For bulls ≥ 3 -years of age approximately twice as many cases of PSDP were detected in polled-breed bulls (13.5%; n=496) compared to horned-breed bulls (5.6%; n=233), clearly indicating that it is a much greater problem in polled-breed bulls but occurs frequently enough in horned-breed bulls to suggest that it is unlikely to be simply associated with the polled gene.
3. From Part 2 of the project the overall prevalence of PSDP in polled-breed bulls (4.4%; n=2,431) was non-significantly greater ($P=0.079$) than in horned-breed bulls (1.5%; n=1,433). With the likely greater use of polled-breed bulls in beef herds, producers of polled-breed bulls should be encouraged to conduct serving capacity tests on their ≥ 3 -year old herd sires to identify those affected with PSDP. Further, with the support of relevant breed societies and geneticists, strategies which may include the use of DNA marker technology should be established to enable seedstock producers to select against this problem.

Contents

1	Background	7
2	Project Objectives	8
3	Methodology	8
4	Part 1 - Review	9
4.1	Overview	9
4.2	Industry concerns regarding the fertility of polled bulls	9
4.3	Anatomy and physiology of penile erection	10
4.3.1	Intromission	12
4.3.2	Ejaculation.....	13
4.4	Premature spiral deviation of the penis (PSDP)	13
4.4.1	Anatomy and physiology relevant to PSDP	13
4.4.2	Aetiology and prevalence of PSDP	15
4.5	Preputial prolapse	18
4.5.1	Anatomy and physiology relevant to preputial prolapse	18
4.5.2	Aetiology of preputial prolapse	19
4.5.3	Heritability and prevalence of preputial prolapse.23Error! Bookmark not defined.	
4.6	The effect of the poll gene on bull serving capacity	22
4.7	A theoretical influence of the poll gene on penile function and fertility	23
4.7.1	The relationship of the poll gene to male infertility in other species	24
4.8	An exploration of the potential effect of the poll gene on a selection of heritable causes of infertility in the bull	24
4.9	A note on persistent frenulum	25
5	Part 2 – Survey of Contemporary Industry BBSE Data	30
6	Discussion	31
7	Success in Achieving Objectives	33
8	Impact of the poll gene on bull fertility – now & in five years time	34
8.1	Impact of the poll gene on bull fertility – Now	34
8.2	Impact of the poll gene on bull fertility – Five years time	34
9	Conclusions and Recommendations	34
9.1	Specific conclusions from the systematic review.....	38
9.2	Suggested areas for further research.....	38
10	Glossary	34

Breeding Soundness Abnormalities in Polled and Horned Bulls

11 **Bibliography** **41**

1 Background

A potential problem highlighted by the MLA funded project AHW.094, 'Genetic options to replace dehorning of beef cattle in Australia' was the possible association between the poll gene and abnormalities affecting the breeding soundness of bulls. Specifically, the conditions of premature spiral deviation of the penis (PSDP), preputial prolapse and reduced serving capacity were identified as having the potential to increase in prevalence with more widespread dissemination of the poll gene throughout the beef cattle industry. One outcome of this review was a recommendation that these associations be further investigated to define the potential magnitude of the problem.

While the literature provides an anatomical mechanism whereby preputial eversion may be associated with the poll gene via inadequacy of the caudal preputial muscles (Long & Hignett 1970; Venter & Maree 1978; Wolfe, Hudson, & Walker 1983), there is no obvious mechanism for the association between the poll gene and PSDP. Thus it is necessary to revisit the detailed anatomy and physiology of the penis during erection and ejaculation in order to identify areas where known poll gene influences, such as abnormalities in muscle development, may affect the risk of PSDP.

In order to avoid missing other potential adverse influences on bull fertility that the poll gene may cause, a protocol was devised to identify other conditions which maybe associated with the polled gene. This was based on the well documented evidence that the polled condition is mainly inherited, with minimal environmental influence. Thus, emphasis was placed on identifying conditions affecting bull fertility where a heritable cause was documented or strongly suspected. This was based on the assumption that any condition likely to be exacerbated by dissemination of the poll gene would likely have a direct, or indirect, heritable aetiology.

This report provides a review of the current state of scientific knowledge of the anatomy of the penis, the physiological events leading to normal erection, intromission and ejaculation and abnormalities affecting bull fertility for which there is strong evidence of a heritable aetiology. It explores the scientific literature and knowledge within the veterinary profession in order to identify any potential association between these abnormalities and the polled condition. A retrospective analysis of data provided by Australian cattle veterinarians and beef cattle researchers who routinely conduct serving ability or serving capacity testing was done to estimate the prevalence of PSDP in beef bulls, and the degree of association with the polled condition.

2 Project Objectives

To:

1. Review the normal anatomy and physiology of the penis and prepuce of bulls.
2. Review the pathogenesis of PSDP and preputial prolapse in the bull, particularly focussing on evaluating the evidence of any association between the polled gene and these abnormalities.
3. Identify breeding soundness abnormalities in bulls which have either a known, or strongly suspected genetic aetiology.
4. Identify heritable abnormalities known to affect the fertility of males in other species.
5. Estimate the prevalence of PSPD and other penile abnormalities in a selected population of polled and horned breed beef bulls in Australia.
6. Provide recommendations to industry on how to minimise the risk of adversely affecting bull breeding soundness by selecting for the polled condition.

3 Methodology

The project was conducted in two parts:

Part 1. A systematic review of the published scientific literature, reports from breed societies in Australia and elsewhere in the world, and unpublished studies from researchers and cattle veterinarians on breeding soundness abnormalities known or suspected to be associated with the poll gene was conducted. This review was conducted by Dr Scott Norman.

Part 2. Analysis of historical data from a selected group of Australian cattle veterinarians and researchers who regularly conduct mating ability/serving capacity testing as part of their bull breeding soundness examinations (BBSE). Three veterinary practices (in north-west and central New South Wales, and south-west Western Australia) and two beef cattle researchers (in Western Australian and Queensland) agreed to provide access to their BBSE databases. Serving capacity data collected by John Bertram, Michael McGowan and Dick Holroyd from bull studs in southern and central Queensland as part of the Bull Power I project (DAQ.104) was also included in the analyses. Each contributed data base was screened to determine the validity of the data – only data recorded for individually identified bulls was used. Only data sets which included owner/manager reported age and, either the horn status or breed of the bulls examined were analysed. The accuracy of the data on breed and horn status was considered high as this was either data supplied by producers/managers for certification of the breeding soundness status of bulls prior to sale, or for research purposes. BBSE data for 6,037 bulls examined between 1991 and 2006 was selected for analysis. The horn status of the majority of bulls (for a small number of bulls there was data on horn status provided by the owner) was estimated from the breed using the same methodology used in AHW.094. Initially the data was collated by practice, but subsequently it was pooled for analysis. The data was collated by breed, age, and breed-horn status and subjected to statistical analyses to establish the strength of relationships between variables.

4 Part 1 - Review

4.1 Overview

In assessing the evidence of any associations between the polled condition and bull reproductive function the following points must be recognised:

1. The scur/horned phenotype can be ambiguous, making accurate phenotypic identification difficult (Prayaga 2007). This means that any producer or veterinary records of bull infertility based on the phenotypic expression of the polled or scurred condition may be inaccurate.
2. The mode of inheritance of the polled condition is still incompletely understood (Prayaga 2007), and thus the importance of any epistatic influences is unknown.
3. The exact locations of the polled, African horned and scur genes in cattle are still unknown. This means that it is difficult to relate the DNA segment that carries these genes and their mutations in cattle to homologous segments of chromosomes in other species. Such information which can be gained by haplotype analysis, would be valuable in assessing theoretical risks associated with the polled condition based on information from other species. Such information from humans has been used to help understand the polled intersex condition found in goats (Vaiman 2000).
4. The mode of action by which the gene combinations produce the polled condition in cattle is still incompletely understood. No references were identified that described the method by which the genes associated with the polled condition in cattle regulate the development of horn buds. In goats, the forkhead transcription factor (FOXL2) plays an integral role in horn bud development and gonadogenesis (Pailhoux, Vigier, & Chaffaux 2001). In its absence, as occurs in the polled condition, there is no horn development and there can be abnormalities in gonadal development. It can be reasoned that interference in the production of this factor (as occurs in the polled condition in goats) may interfere with other tissues of ectodermal origin.

In the light of these gaps in our understanding of the condition, the approach used to identify potential abnormalities associated with the polled condition was:

1. Identify industry concerns about the fertility of polled bulls based on science or anecdote.
2. Explore any scientific data that may support these concerns and identify possible mechanisms by which the poll gene may be involved.
3. Review bull reproductive tract anatomy and function focussing on structures and tissues potentially influenced by the poll gene.

4.2 Industry concerns regarding the fertility of polled bulls

Specific beef industry concerns regarding the breeding of polled bulls have been circulating for many years. The earliest scientific reference that could be identified suggesting reproductive problems occurred more commonly in polled bulls was a clinical review of penile and preputial problems (Milne 1954). Importantly, this was a review based mainly on anecdote from the author rather than on statistical analysis of data.

Concerns regarding the use of polled animals probably have been perpetuated by the findings of studies identifying deficiencies in production traits such as milk quality, weight gain and meat quality. A study of the German Fleckvieh breed (Lamminger *et al.* 2000), found that there were demonstrable effects of the polled condition on economically significant production traits including reduced milk, fat and protein yield. This suggests that there may be a direct effect of

Breeding Soundness Abnormalities in Polled and Horned Bulls

the poll gene on these traits and that the industry needs to be vigilant in identifying other possible adverse influences of the polled condition.

More recently, Australian beef industry concerns regarding polled animals have been summarised (Prayaga 2005). With regard to bull fertility, these included:

1. The perception that the poll gene is associated with an increased prevalence of the condition of premature spiral deviation of the penis (PSDP).
2. The perception that the poll gene is associated with an increased prevalence of preputial prolapse.
3. The perception that polled bulls have reduced serving capacity (libido) compared to horned bulls.

These specific concerns will be addressed in this report.

4.3 Anatomy and physiology of penile erection

In order to clearly understand the pathogenesis of PSDP, it is considered necessary to have an understanding of the normal events leading to penile erection, intromission and ejaculation. The nomenclature used in this report follows that used by (Ashdown 2006), which is largely based on that described in *Nomina Anatomica Veterinaria* (International Committee on Veterinary Gross Anatomical Nomenclature 1994) except for a few small modifications (Figure 1).

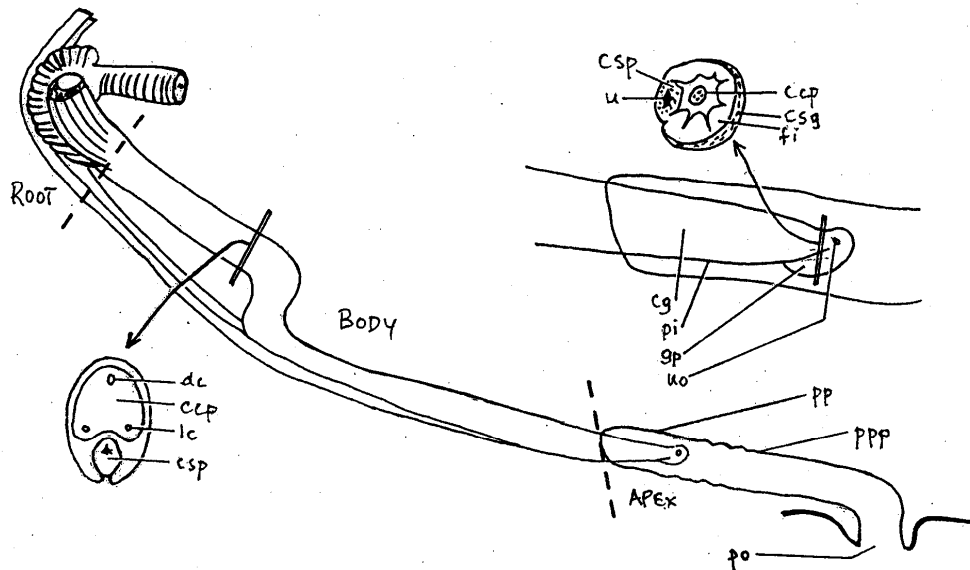


Figure 1 - Anatomy of the bovine penis: ccp, corpus cavernosum penis; cg, collum glandis; csg, corpus spongiosum glandis; csp, corpus spongiosum penis; dc, dorsal canal; fi, fibrous tissue of gp; lc, lateral canal; pi, penile integument; po, preputial orifice; pp, penile part of prepuce; ppp, prepenile part of prepuce; u, urethra; uo, urethral orifice. Reproduced with permission (Ashdown 2006).

Breeding Soundness Abnormalities in Polled and Horned Bulls

There are a number of good reviews of the functional anatomy of the bovine penis. Most have involved, or referred to, the work of Ashdown, who has spent a lifetime researching this field. The following review of the events leading to erection and ejaculation is based on one of Ashdown's many articles, which is a summary of his research and that of others relevant to the field (Ashdown 2006).

During sexual arousal in the bull, pressures in the corpus cavernosum penis (ccp) and corpus spongiosum penis (csp) rise from approximately 16 mm Hg to subsystolic levels of approximately 77 mm Hg in the ccp (Beckett *et al.* 1974b). While the penis begins to straighten, this pressure is inadequate for intromission. These changes are due to relaxation of smooth muscle in a number of structures including:

- The walls of the penile artery and its branches to the ccp (deep artery) and csp (artery of the bulb) (Gilanpour 1972).
- In the muscular walls of the cavernous spaces of the crura and bulb of the penis.
- The muscles of the longitudinal and connecting canals of the ccp within the penile body.

It is probable that at this stage there is some reduction in deep venous drainage from the crura by the mechanism demonstrated in man (Kiss 1921) and the dog (Fournier *et al.* 1987). These authors demonstrated that filling of the larger central cavernous spaces of the crura squeezes the small peripheral spaces lying against the thick tunica albuginea, reducing the venous drainage from these peripheral spaces. The retractor penis muscle (which is smooth muscle) also relaxes, which means the process of sexual arousal brings the bull to a state where erection sufficient for intromission can be rapidly achieved provided there is further stimulation and opportunity. During this period of sexual arousal, emission of semen into the pelvic urethra is also stimulated, in preparation for ejaculation, which in the bull occurs almost immediately after intromission.

The mechanism for erection of the bovine penis to the point of intromission is summarised in Figure 2. When the bull mounts the cow or teaser animal and protrudes a length of straight and erect penis, the pressure within the ccp required for this is well above systolic pressures (Beckett *et al.* 1974b) and cannot be attained by the autonomic neuromuscular mechanisms of "teasing". Pumping of the tail head is visible and contractions of the perineal muscles can be palpated. The paired deep penile arteries are large terminal branches of the penile arteries. They supply the cavernous spaces of the crura and the first few centimetres of the penile body (Ashdown *et al.* 1979; Gilanpour 1972). Dilation of these arteries during sexual stimulation (Gilanpour 1972) can rapidly fill the cavernous spaces of the crura. The ischiocavernosus muscles overlay the crura, and radiographs during electroejaculation show compression of the crura and transfer of the contents of the crural cavernous spaces into the cavernous spaces of the body of the ccp. At the same time the penile vein, lying just cranial to the crura, and its deep penile branches which drain the crura, are compressed and emptied (Gilanpour 1972). Thus, increased ccp pressure during natural service (Beckett *et al.* 1972a) and electroejaculation (Beckett *et al.* 1972b) is achieved by rhythmic pumping of the ischiocavernosus muscles which expels blood from the crura into the body of the ccp. At the same time the deep penile artery and vein of the crura are compressed and occluded against the ischiatic arch. The whole of the venous drainage from the ccp is through the deep penile veins. There is no distal venous drainage of the ccp in the bull (Ashdown & Gilanpour 1974; Gilanpour 1972). During contraction of the ischiocavernosus muscles, when the crura are compressed and the deep penile artery and vein are occluded, the cavernous spaces in the body of the ccp are a closed system except for the small branches of the dorsal artery that penetrate the tunica albuginea and supply the cavernous spaces (Ashdown *et al.* 1979; Ashdown 2006). In the bull, Beckett *et al.* (1974a) recorded rhythmic high pressure peaks from the ccp during natural service and before ejaculation, with a

Breeding Soundness Abnormalities in Polled and Horned Bulls

mean peak pressure of over 14,000 mm Hg, correlated with intense activity of the ischiocavernosus muscles. The ccp pressure remained higher than systemic arterial pressure for an average of 8.4 seconds (systolic pressure during coitus averaged 237 mm Hg).

The filling of the crura and the elevated (subsystolic) ccp pressure that result from "teasing" ensure that pumping by the ischiocavernosus muscles can quickly supply the volume of blood needed to obtain erection pressures within the ccp. In excised bull penises, 80 mL of warm saline were sufficient to raise ccp pressure from 0 - 200 mm Hg (approx. systolic blood pressure during coitus) and only 127 mL was needed to increase pressure to 7,500 mm Hg (Beckett *et al.* 1974a). This shows the efficiency of the vascular mechanism of erection in the bull.

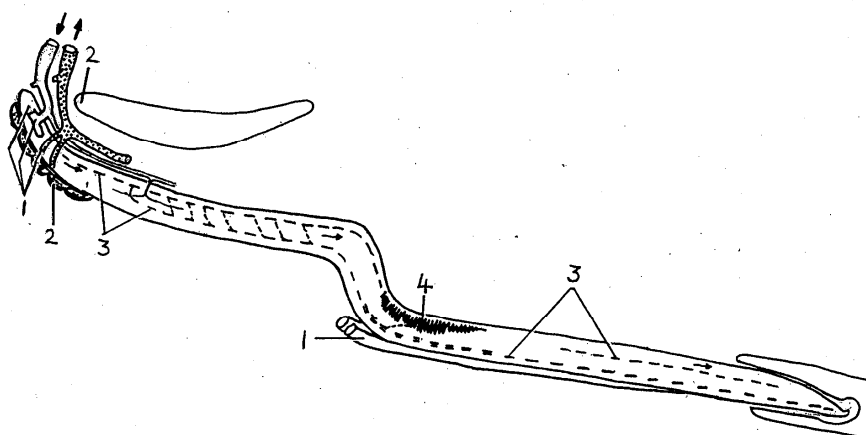


Figure 2 - The mechanism of penile erection in the bovine. 1: During the Subsystolic Phase, there is relaxation of penile smooth muscle. Increased arterial flow in the deep penile arteries and reduced venous return from the deep veins ensure filling of the cavernous spaces of the crus, raising pressure within the ccp. Retractor penis muscles relax. 2: The ischiocavernosus muscles rhythmically compress the crura against the ischiatic arch and rhythmically occlude the deep penile arteries and veins. 3: During the Suprasystolic Phase, blood is pumped from the crura through the longitudinal canals of the ccp (small arrows) distally to produce very high peaks of pressure in the ccp. Stiffening and elongation results in protrusion of the penis. 4: During the Fourth Phase, there is filling of specialised cavernous tissue at the distal sigmoid flexure which results in straightening of the penis in preparation for intromission. 5: Once intromission and ejaculation have occurred, the ischiocavernosus muscles cease pumping. Penile vascular smooth muscle contracts and blood drains from the ccp via its crura and the deep penile veins. The sigmoid flexure re-forms as pressure in the ccp returns to resting levels. The retractor penis muscles contract and the penis become shorter and flaccid prior to repositioning within the prepuce. Used with permission (Ashdown 2006).

4.3.1 Intromission

After a period of sexual arousal, the bull prepares to mount. Just before, or during mounting, the penis is protruded, erect and straight, from the preputial orifice. The cranial preputial muscle relaxes its sphincteric action (Ashdown & Pearson 1973a; Larson, Kitchell, & Campbell 1961) allowing unimpeded protrusion of the penis. The protruded collum glandis (pars libera) is covered by its penile integument and the rest of the protruded penis is covered by the everted penile and prepenile parts of the prepuce.

Just prior to intromission the shape of the collum glandis of the erect penis varies between bulls. Photographs of bulls at AI centres (Ashdown & Majeed 1976) show that the urethral process lies

Breeding Soundness Abnormalities in Polled and Horned Bulls

on the right hand side and the urethral orifice may face dorsally, ventrally, or most commonly, laterally. The terminal 2-3 cm may deviate ventrally through nearly 45° in apparently normal bulls. The mounted bull positions its hind feet close to the cow or teaser animal. The penis then makes rapid to and fro movements, searching for the vulva or artificial vagina (AV). These movements probably result from pressure changes in the ccp, produced by the pumping action of the ischiocavernosus muscles (Watson 1966). Intromission should immediately follow but may, in some bulls, be delayed by repeated "searching". Both superficial and deeper nerve endings on the glans penis mediate the tactile stimuli necessary for intromission (Beckett, Hudson, & Walker 1978). Mechanoreceptors of the dorsal penile nerve (mainly slow-adapting) occur over the surface of the glans penis, penile integument, and penile and prepenile parts of the bovine prepuce (Cottrell, Iggo, & Kitchell 1978). It is possible that, in the bull, the cranial, middle and caudal preputial nerves (Larson & Kitchell 1958) could contribute to "searching", but unilateral and bilateral neurectomies (Beckett, Hudson, & Walker 1978) suggest that the dorsal nerves of the penis are the main sensory nerves for "searching" and intromission in the bull. It has been found that sensory nerve endings were far more numerous on the collum glandis and glans penis than on the penile or prepenile parts of the prepuce (Izumi 1980).

4.3.2 Ejaculation

On achieving intromission, the bull flexes the lumbar vertebrae, contracts the abdominal muscles, and extends the hind limbs. The resultant movement may lift the hind feet off the ground. The intromittent penis is protruded to its greatest extent in the thrust, and ejaculation occurs with marked pumping of the tail head. Using a transparent AV, it has been found that ejaculation occurred approximately one second after intromission, with a protruded penile length of about 50 cm. Ejaculation lasted for 0.3 of a second. In more than 50% of cases the collum glandis spirals at ejaculation, spraying semen around the wall of the AV (Seidel & Foote 1969).

4.4 Premature spiral deviation of the penis (PSDP)

4.4.1 Anatomy and physiology relevant to PSDP

Figure 3 shows the fibroarchitecture of the bovine penis in relation to spiral deviation of the collum glandis. In particular, note the location of the dorsal apical ligament, labelled in the diagram as dl¹.

Breeding Soundness Abnormalities in Polled and Horned Bulls

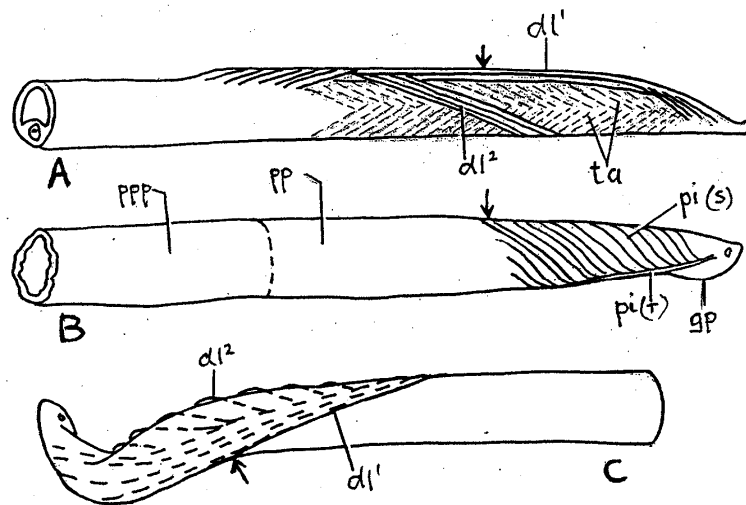


Figure 3 - The fibroarchitecture of the bovine penis in relation to spiral deviation of the collum glandis (pars libera). Arrows mark the proximal limit of the pars libera. (A) right lateral view of the distal penis with integument removed. dl^1 represents the thick portion of the dorsal apical ligament. dl^2 represents the thin portion of the ligament, which is partially removed to expose the deeper tunica albuginea of the penis, ta. (B) Integument intact demonstrating the glans penis, gp; longitudinal fibres of the penile integument at the raphe, pi(r); penile integument with spiral fibroarchitecture, pi(s); penile prepuce, pp; and prepenile prepuce (ppp). (C) left lateral view of a spirally deviated pars libera penis with integumentary coverings removed. The deviation is to the right with the thick portion of the dorsal apical ligament displaced to the left and ventrally. The thin portion of the dorsal apical ligament is stretched over the dorsal, convex surface. Used with permission (Ashdown 2006).

It is usually assumed that deviation of the protruded erect penis will result in difficulties at natural service. Simulated erection of excised penises from 25 bulls with no known problems at service showed slight to moderate ventral (2), left lateral (3) and right lateral (3) deviations distal to the sigmoid flexure (Maleed 1976). The terminal 20 cm of the penis has a special modification of the dorsal longitudinal fibres of the tunica albuginea (Ashdown & Smith 1969) known as the dorsal apical ligament. When this asymmetrical dorsal apical ligament was removed, simulated erection resulted in marked ventral deviation ($10-36^\circ$) in 20 and marked lateral deviation ($10-52^\circ$) in 24 of the 25 excised specimens tested (Maleed 1976). Importantly, the straightness of the erect distal penis as the bull mounts is controlled by this dorsal apical ligament. Surgical removal of the ligament results in penile deviation ventrally and to the right (mimicking the condition of PSDP), and intromission becomes impossible (Ashdown & Pearson 1971).

Diagnosis of PSDP depends on visualisation of the condition, ideally during a 20 minute serving ability/capacity test. No relationship has been identified between spiral deviation observed during electroejaculation and PSDP. Thus, observation of repeated natural service is considered essential for the diagnosis of this condition.

The libido of affected bulls may progressively decrease due to their inability to gain intromission. This point is critical, as it seems that the beef industry has inappropriately made an association between the polled condition and reduced serving capacity (libido) based on an incorrect interpretation of the Australian study which associated PSDP with the polled condition (Blockey

& Taylor 1984).

4.4.2 Aetiology and prevalence of PSDP

When a bull serves a cow, there are many processes which must occur in tight synchrony in order for semen to be successfully deposited into the anterior vagina. The penis must be maintained in an erect, linear condition during searching for the vulval opening and intromission into the vagina. This is achieved in part due to the stabilising function of the dorsal apical ligament of the penis. Once intromission has been gained, blood pressure within the corpus cavernosum and corpus spongiosum increases dramatically to the point where the dorsal apical ligament may no longer maintain the tip of the penis in a straight line. The result is that in many bulls, the tip of the penis normally spirals to the right at the time of the ejaculatory thrust. Thus, spiral deviation of the penis is a normal event at the time of ejaculation. PSDP occurs when this spiralling event occurs prior to the penis gaining intromission into the vagina. The spiralled (corkscrewed) end of the penis then acts as a physical barrier to the penis entering the vulval lips, as the cross-sectional diameter of a spiralled glans penis can be approximately 6 cm (Seidel & Foote 1969).

PSDP is considered to be due to progressive degeneration of the dorsal apical ligament of the penis, with the attachment between the dorsal apical ligament and the tunica albuginea of the penis becoming less intimate as the bull ages. An understanding of the progressive nature of this condition is useful in identifying affected bulls. Younger bulls with PSDP may only display the abnormality in less than 25% of services. Thus, affected bulls may go undetected until their second or third joining season. The condition commonly progresses with age until almost 100% of service attempts are affected by PSDP. PSDP currently can only be detected by observing bulls attempting to serve females either in a yard test or at pasture. Because of the speed of service (occurs within seconds of mounting) detection is best done in a yard test using restrained females and with the observer standing on the right hand side of the bull. Occasionally during electroejaculation a bull's penis is observed to spiral. The current recommendation is that bulls that spiral during electroejaculation should be examined in a serving ability/service capacity test for signs of PSDP. There have been several reports of cases of PSDP in which the bull showed spiralling of the penis during electroejaculation (Bertram pers com).

Prevalence of PSDP over all bull breeds has been reported to range from 2% to 10% (Bertram, Smith, & Foote 1993; Blockey & Taylor 1984; Carroll, Ball, & Scott 1963; McDiarmid 1981). However, in individual herds, prevalences as high as 27% have been documented (Blockey & Taylor 1984). In a search of the literature over the last 60 years, perhaps the first scientific paper that suggested there may be an increased prevalence of PSDP in polled breeds dates back to 1954 (Milne 1954). However, this paper did not offer any data or references to support this claim, simply the authors' opinion. The direct quote is "Since it (PSDP) seems to be most commonly encountered in polled breeds, an inherited tendency has been suspected. In these animals there appears to be a natural weakness which leads to a downward, or less commonly, a lateral or spiral deviation. It has also been observed in young bulls, not necessarily of the polled breeds, without any history of trauma". It is interesting that this paper suggested that downward deviation of the penis was most commonly associated with the polled condition, with lateral deviation and PSDP less common. Possible interpretations of this are that the authors' opinions were incorrect, genetics have changed dramatically over the last 50 years, or subsequent authors have misrepresented this statement by focussing on PSDP and ignoring the other forms of penile deviation. There is also no suggestion it is associated directly with the poll gene, but simply recognised more frequently within the polled breeds. If true, this may be more

Breeding Soundness Abnormalities in Polled and Horned Bulls

a reflection of the initial genetic pool for these breeds, rather than a direct link with the polled condition.

In 1963 a large retrospective study involving examination of the BBSE findings of almost 11,000 bulls reported an overall prevalence for PSDP of 1.7% (Carroll, Ball, & Scott 1963). This study included over 6,800 Hereford bulls and over 2,600 Angus bulls. Unfortunately, the description of the materials and methods is not clear and it is difficult to determine exactly how many of these bulls were actually observed during service. The authors state that “most bulls were collected using electroejaculation, while in a few instances, the artificial vagina was used”. However they did record 190 cases of PSDP that were identified at natural service. The authors did not report that PSDP was more or less prevalent in the polled breeds.

The second report of a link between PSDP and the polled condition was derived from an anatomical study conducted in 1973 (Ashdown & Pearson 1973b). This study documented 27 cases of PSDP and found that 16 of the cases were in naturally polled bulls (11 cases were in Polled Hereford). Interestingly, this also means that 11 of the 27 cases were in naturally horned bulls. Unfortunately, this study was based solely on the 27 PSDP cases presented to the authors referral clinic and so no prevalence data specific to each population is available to assist in determining the significance, or relevance of these findings. While the authors make a case for PSDP being associated with the polled condition, it seems more likely that if any conclusion can be drawn at all from this study, it is that there may be a tendency for PSDP to be associated with breed. These authors provided circumstantial evidence that the condition could be heritable (three of the eleven affected Poll Hereford bulls were related to each other), and this lends weight to the argument that it is a breed condition rather than being specifically related to the poll gene. However there is very little scientific data to confirm the heritability of PSDP (Steffen 1997). Thus, the conclusion that PSDP is a heritable condition is currently based more on anecdote than the findings of any appropriately designed and analysed study. There is anecdotal evidence that some cases may be the result of trauma, however it is difficult to differentiate clinically between traumatic and congenital causes. Therefore, the conservative recommendation is to consider cases of PSDP as heritable until further evidence is presented.

A third study that has implicated an increase in the prevalence of PSDP in polled bulls reported that 19 out of 181 (10.5%) Angus bulls older than three years of age had PSDP (McDiarmid 1981). This study examined a total of 278 bulls, 220 of which were Angus, with 39 of those being two year olds. While no mention is made of the relationships between these Angus bulls, it is noted that they were all owned and managed by a County Lands and Survey Department, meaning that there was significant potential for many to be related. While the study also examined other breeds, unfortunately the numbers were too small to make valid between-breed comparisons. The largest representation of non-Angus bulls was 50 Hereford bulls. However 12 of these were two year olds, meaning that only 38 of the Hereford bulls could be validly compared to the older Angus bulls. While the fact was that none of the older Hereford bulls had PSDP, there is insufficient data to support the authors' conclusion that older Angus bulls are more prone to PSDP compared to other breeds. In contrast, more contemporary anecdote from practitioners performing thousands of serving capacity assessments has failed to make such an association (R. Holmes *pers. comm.*). Importantly, McDiarmid (1981) presents no evidence that the condition may be associated with the poll gene, only circumstantial evidence that it may be more prevalent in the Angus breed. The fourth study that could be identified implicating a link between the polled condition and PSDP was a large study conducted in Australia (Blockey & Taylor 1984). This study was based on serving capacity data from over 1,000 bulls, including 415 Angus bulls, 167 Poll Hereford bulls, and 448 Hereford bulls. The remainder were Poll Shorthorn, Red Poll and Murray Grey bulls. The prevalence of PSDP in the polled breeds compared to horned breeds was 16% and 1%, respectively. In Poll Hereford and horned

Breeding Soundness Abnormalities in Polled and Horned Bulls

Hereford bulls the prevalence was 10% and 1%, respectively. While no familial data was presented on the relationships of the Poll Hereford and Hereford bulls, when Blockey and Taylor (1984) examined the relationship of affected Angus bulls, they found “a high degree of common ancestry between bulls at the first, second and third generation”. While this adds more weight to a possible heritable nature of the condition, it also strengthens the suggestion that PSDP is a breed-related condition rather than being specifically associated with the poll gene. Unfortunately, Blockey and Taylor (1984) were unable to provide heritability estimates for PSDP from their data.

PSDP is a progressive and degenerative condition; therefore the literature was explored to identify studies specifically examining the prevalence of PSDP in older bulls. Only one study could be identified, which reported the prevalence of PSDP in four year old Santa Gertrudis and Belmont Red bulls as 1.8% and 13.5%, respectively (Bertram 1999). This was an Australian study involving the serving capacity testing of 558 Santa Gertrudis and 335 Belmont Red bulls over a five year period. While two other breeds were also studied, there were insufficient animals to make meaningful comparisons. Belmont Red cattle were originally derived from Africander (50%), Shorthorn (25%) and horned Hereford (25%) (Australian Meat & Livestock Corporation 1989). However, the Belmont Red breed society has allowed Angus cross, Brahman cross and Bonsmaras to be graded up to Belmont Red cattle, and thus some Belmont Red bulls may be polled. Further, a study of PSDP in Limousin bulls (horned animals) found a prevalence of PSDP of 26% (Bertram, Smith, & Foote 1993).

Apart from the study by Blockey & Taylor (1984), there is very little scientific evidence to support a specific association between the poll gene and PSDP. The paper by Ashdown and Pearson (1973b) has been widely cited, with one very influential text using this reference as proof of the link between the polled condition and PSDP (Roberts 1986). Thus, it is easy to understand how the beef industry and the veterinary community have become concerned about the possible link between the polled condition and PSDP. It would appear that the two studies by Bertram (1993, 1999) place these older assertions under some significant doubt.

4.5 Preputial prolapse

4.5.1 Anatomy and physiology relevant to preputial prolapse – don't put figure straight after heading

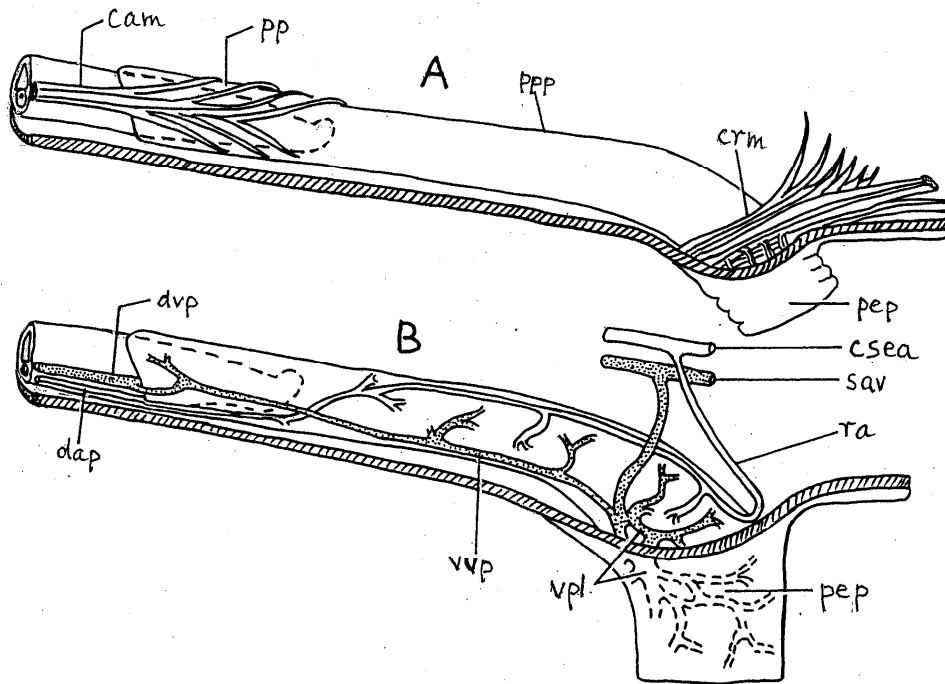


Figure 4 – (A) Right lateral view of muscles of the bovine prepuce: cam, caudal (retractor) preputial muscle; crm, cranial (protractor) preputial muscle; pp, penile portion of prepuce; ppp, prepenile portion of prepuce. Used with permission (Ashdown 2006).

The prepuce is the hairless, pink skin contained within the hair-covered sheath and can be considered as a derivative of the skin of the abdominal wall. It is controlled by striated muscles derived from the cutaneus trunci muscle (Ashdown 2006). These originate from the deep fascia of the abdominal wall and insert onto the outer fibrous layer of the preputial wall (Ashdown & Pearson 1973a). The cranial (protractor) muscles arise from the abdominal tunic in the region of the xiphoid cartilage (Long & Hignett 1970) and encircle the most cranial, pendulous part of the prepuce and exert a sphincteric action on the preputial orifice. They also insert into the dermis of the skin around the orifice and can shorten the pendulous part of the prepuce. The caudal muscles of the prepuce each originate from two separate sites. The lateral origin is from the dense layer of fascia that leaves the lateral edge of the external inguinal ring and runs into the scrotum to form the scrotal fascia. The medial origin is from the medial aspect of the scrotal septum, near its point of origin from the yellow elastic lamina of the abdominal wall. The caudal preputial muscles insert into the connective tissue just below the dermis of the penile prepuce over a large area, approximately 10 cm in length.

4.5.2 Aetiology of preputial prolapse

A clear definition of both preputial eversion and preputial prolapse is needed in order to review our current understanding of the aetiology of preputial prolapse and the possible involvement of the poll gene. This is particularly important, as one significant article (with regard to impact factor) was identified where the authors appear to have confused these two conditions and incorrectly reported the prevalence of preputial eversion as preputial prolapse (Venter & Maree 1978). The error resulting from this confusion is massive. This paper is widely referenced and states that preputial prolapse is recorded in up to 85% of polled bulls and only 1.4% of horned bulls. Investigation of their reference for this claim (Long 1969) revealed that up to 85% of polled bulls demonstrated preputial eversion during a specified period of observation. Contrary to Venter and Maree's interpretation, Long specifically stated that study of the health records of bulls which habitually everted the prepuce failed to reveal a greater occurrence of preputial disease compared to those bulls that did not evert the prepuce. Errors of interpretation such as that by Venter and Maree have apparently resulted in significant misunderstandings within the industry. Preputial **eversion** occurs when a variable length of normal prepuce protrudes temporarily from the preputial orifice and can be readily retracted back into the sheath by the bull (Long 1969). The important point is that this is a voluntary action. It is not considered pathological, and is considered by some to assist with body temperature control in some breeds (Grove 1968). Preputial **prolapse** is where a variable length of pathologically affected prepuce protrudes from the preputial orifice and is unable to be voluntarily retracted within the sheath.

The poll gene has been strongly linked to a deficiency in the development of the caudal preputial muscles, and a higher prevalence of preputial eversion in polled *Bos taurus* breeds (Bruner & Van Camp 1992; Long & Hignett 1970; Rice 1987) and in *Bos indicus* breeds (Turner 2007a). Study numbers are usually small, however in one significant study comparing 275 polled bulls to 210 horned bulls, the reported prevalences of preputial eversion in polled versus horned animals were 81% and 64% respectively (Long & Dubra 1972). Interestingly almost 70% of 169 horned Hereford bulls everted their prepuce in this study suggesting that the effects of the poll gene and its influence on the development of the caudal preputial muscles is not the only influence on whether or not preputial eversion occurs. No other anatomical differences between the prepuces of polled and horned bulls have been reported except for the somewhat surprising finding that horned bulls had a significantly larger mean volume of prepuce compared to polled bulls (Long & Hignett 1970). This suggests that preputial eversion can not be readily explained simply by the presence of excess preputial epithelium and adds credence to the role the caudal preputial muscles and sheath structure may play in maintaining control of the prepuce within the sheath.

The link between preputial eversion and preputial prolapse, although intuitive, is equivocal, with some workers strongly suggesting that frequency of eversion is not related to the prevalence of clinical prolapse in *Bos taurus* breeds (Long & Dubra 1972). A number of factors have been suggested as being involved in the aetiology of preputial prolapse (Venter & Maree 1978). These include injury, external parasites, infection, functional and anatomical abnormalities of the prepuce and caudal preputial muscle, inefficient caudal preputial muscle action, pendulous sheath (Wolfe, Hudson, & Walker 1983), size of the preputial orifice, longer preputial length (van den Berg 1984), excessively pendulous sheath and angle of the opening of the sheath (Aehnelt 1951; Ashdown 2006), and genetic predisposition. It has been suggested that *Bos indicus* and polled breeds in general have increased susceptibility to the condition (Venter & Maree 1978). While there appears to be strong data to suggest polled bulls have poorly developed caudal preputial muscles it is also apparent that management conditions and sheath structure are likely to play a significant role in the development of a pathological prolapse. One avenue that does not appear to have been investigated is the role of hormones such as oestrogen in the aetiology

Breeding Soundness Abnormalities in Polled and Horned Bulls

of the condition. In feedlot steers, preputial prolapse has been associated with an abnormal response to hormonal growth promotants. There is the possibility that bulls more prone to prolapse may have higher oestrogen production from the Sertoli cells or more oestrogenic receptors within the prepuce. Phyto-oestrogens from feed may also play a role in the aetiology of preputial prolapse.

While studies in *Bos taurus* breeds suggest that deficiency in the caudal preputial muscle and preputial eversion are not likely to be related to prevalence of preputial prolapse (Long & Dubra 1972), there is the suggestion that this may not be the case in *Bos indicus* breeds. Many of the studies on preputial prolapse in *Bos indicus* breeds include significant representations of the Santa Gertrudis breed. However, it can not be concluded that other breeds such as Droughtmasters do not have a significant prevalence of the condition. The breed representation in these studies likely reflects the world-wide distribution of the Santa Gertrudis breed and its subsequent exposure to research. In one study, preputial prolapse in Santa Gertrudis bulls was reported to occur in up to 30% of 4 year old animals (Venter & Maree 1978). This high prevalence of prolapse in the Santa Gertrudis breed is supported by a report of cases presented for surgery where 19 of the 20 cases were Santa Gertrudis bulls (Donaldson & Aubrey 1960). While Santa Gertrudis are based on a cross of 3/8 Brahman and 5/8 Shorthorn and considered to be a predominately horned breed (Prayaga 2005), polled animals do exist in this breed (Santa Gertrudis Breed Society 2007). In 2002, it was estimated that 15% of Santa Gertrudis bulls were polled (Santa Gertrudis Breed Society 2007). However, in many cases the horn status of bulls at the time of dehorning is not recorded. A small 1998 abattoir study (Turner 2007a) of 23 Santa Gertrudis bulls with preputial prolapse in which the horned status was known found that:

- Eight of the 23 bulls were polled, which means that polled bulls were over represented in the prolapse group (35%) compared to the estimated prevalence of the poll gene within the breed at the time of the study (5%).
- Seven of the eight polled bulls (88%) were less than six years of age when culled for preputial prolapse compared to seven of 15 (47%) horned bulls.
- All but one of the polled bulls had a small, or absent caudal preputial muscle.

In this study, there is evidence of an increased prevalence of preputial prolapse associated with the poll gene and reduced development of the caudal preputial muscles in a *Bos indicus* derived breed. This is in contrast to the apparent situation in *Bos taurus* breeds. *Bos indicus* derived breeds are reported to have a significantly longer preputial length and a larger preputial orifice compared to *Bos taurus* breeds (van den Berg 1984). They also tend to have a sheath opening which more commonly points directly downward (Ashdown 2006; van den Berg 1984).

Although *Bos taurus* breeds are considered less susceptible to preputial prolapse compared to *Bos indicus* derived breeds, the Hereford breed has been identified as the *Bos taurus* breed most susceptible to prolapse (Roberts 1986). Preputial prolapse appears to be extremely rare in Shorthorns and their crosses (Lagos & Fitzhugh 1970), with only a low prevalence being recorded in cross-bred Santa Gertrudis bulls where the maternal grandmothers were Shorthorns (Venter & Maree 1978).

From these studies, it appears that preputial eversion and the presence or absence of the caudal preputial muscles has minimal association with preputial prolapse in *Bos taurus* breeds. However, there is some evidence to suggest that preputial eversion in association with longer preputial length, a larger preputial orifice and a sheath opening which points directly downward as is found more commonly in *Bos indicus* derived breeds may contribute to the occurrence of preputial prolapse.

4.5.3 Heritability and prevalence of preputial prolapse

The heritability of preputial **eversion** calculated from 113 second-cross ($\frac{3}{4}$ Santa Gertrudis, $\frac{1}{4}$ British) bulls is considered to be approximately 0.35 (Lagos & Fitzhugh 1970). While these authors reported the figure as the heritability of preputial **prolapse**, close examination of their study revealed that they were, in fact, monitoring preputial eversion. While the standard error of this estimate is quite high it can be concluded that the prevalence of preputial eversion (the condition directly associated with reduced function of the caudal preputial muscle in polled bulls) can be reduced by culling affected bulls. This can be done at a relatively young (approximately 18 months) age. Significant differences in the prevalence of preputial eversion in the progeny of different sires have been reported (Lagos & Fitzhugh 1970) and confirm the potential effectiveness of this method of control. By applying accepted breeding principles, it would be expected that rapid reduction in the prevalence of preputial eversion could be made by using a one hour observation test of groups of bulls as described by Lagos & Fitzhugh (1970). While there is minimal evidence that preputial eversion is directly linked with an increased prevalence of preputial prolapse in *Bos indicus* derived breeds, it is intuitive that a bull prone to eversion, that also has an excessively pendulous sheath with a sheath opening facing vertically toward the ground, might have an increased risk of preputial prolapse. Therefore, combining observation for preputial eversion with selection of bulls without an excessively pendulous sheath may reduce the prevalence of preputial prolapse.

Data on the prevalence of preputial prolapse in beef bull populations is difficult to find due to the lack of specific survey data and apparent confusion in the literature regarding the definition of preputial prolapse and preputial eversion. One unpublished 1998 survey of 6,040 bulls on eight north Australian cattle properties found that annual bull wastage from all causes was 15% (n=900 bulls) (Turner 2007b). Of the 900 bulls culled, 252 (28%) were due to reproductive problems, 108 (12%) had damaged penises and 81 (9%) were recorded as having “damaged” prepuces. While this doesn’t give an exact prevalence of preputial prolapse, it can be inferred that the overall annual prevalence in this bull population is approximately 1%. Further, amongst bulls culled from these properties the prevalence of preputial prolapse in Santa Gertrudis bulls (2.8%; n=541) and Brahman bulls (4.1%; n=271), was similar. Another survey of culled bulls at a Western Australian abattoir found that 34.3% had pathology affecting the testicles, epididymides, penis or prepuce (Bellenger 1971).

Breeding Soundness Abnormalities in Polled and Horned Bulls

Table 1. Summary of breed specific cattle numbers from historical breed society records according to horns status (Kishore, 2007). Percentages (rounded to nearest decimal) are given in parentheses

Breeds	Horned	Scurred	Polled	Unknown	Total
Hereford and Polled	1204881	28392	1160271	28145	2421689
Hereford*	(49.8)	(1.2)	(47.9)	(1.2)	
Brahman	469287	708	67978	137596	675569
	(69.5)	(0.1)	(10.1)	(20.4)	
Santa Gertrudis	477181	3532	31628	6779	519120
	(91.9)	(0.7)	(6.1)	(1.3)	
Droughtmaster	55815	12992	142574	92	211473
	(26.4)	(6.1)	(67.4)	(0.0)	
Shorthorn	19575	238	4	372815	392632
	(5.0)	(0.1)	(0.0)	(95.0)	
Braford	0	3962	35549	117325	156836
	(0.0)	(2.5)	(22.7)	(74.8)	
Brangus	559	19	47385	2749	50712
	(1.1)	(0.0)	(93.4)	(5.4)	
Simmental	1243	1579	27781	307987	338590
	(0.4)	(0.5)	(8.2)	(91.0)	
Belmont Red	6399	703	5557	38020	50679
	(12.6)	(1.4)	(11.0)	(75.0)	
Limousin	103504	2042	28629	111521	245696
	(42.1)	(0.8)	(11.7)	(45.4)	
Charolais	42014	2335	31675	140117	216141
	(19.4)	(1.1)	(14.7)	(64.8)	

The only published data on the prevalence of preputial prolapse was a figure of 0.4% reported from a longitudinal study on 485 bulls comprising 214 Angus, 52 Poll Hereford, 169 horned Hereford, 7 Polled Brangus, 17 horned Brangus, 2 horned Shorthorn, 7 Charolais, 11 Friesian, 3 Santa Gertrudis, 1 Brahman cross and 2 Charolais cross (Long & Dubra 1972). In this study, the only two cases of preputial prolapse recorded were in Santa Gertrudis bulls. There is a clear need for a systematic survey of the prevalence by breed of abnormalities affecting the reproductive function of bulls in both northern and southern Australia.

4.6 The effect of the poll gene on bull serving capacity

No papers were identified associating the polled condition with reduced serving capacity. Importantly, one study had an ambiguous conclusion which has apparently confused readers unfamiliar with the PSDP condition and the serving capacity test (Blockey & Taylor 1984). This paper concluded “that spiral deviation of the penis can be accurately diagnosed by the serving capacity test, it depresses the serving capacity of bulls and its prevalence in polled beef breeds in 2 Australian states was high” (Blockey & Taylor 1984). This paper may have initiated the misconception of poor libido in polled bulls. Readers of this paper may have developed the thought process that PSDP is associated with the polled condition, and bulls with PSDP have reduced serving capacity, *ergo*, bulls with the polled condition have reduced serving capacity. Thorough reading of the Blockey paper confirms this is a false conclusion to draw. Examination of the literature for sheep supports the conclusion that the polled condition is not associated with lower libido. In a study comparing plasma testosterone concentrations in Poll Dorset rams with

Breeding Soundness Abnormalities in Polled and Horned Bulls

horned rams, the Poll Dorset rams showed an extended period of higher plasma testosterone compared to the other breeds (D'Occhio & Brooks 1983).

The conclusion is that there is no published evidence to suggest that the poll gene or the polled condition adversely affects serving capacity in bulls.

4.7 A theoretical influence of the poll gene on penile function and fertility

Unfortunately, most of the original studies of horn development in cattle were published in German (Brandt 1928; Siegert 1955), therefore there is a dependence on English reviews and interpretations of the original literature.

Horn development in cattle commences as early as 90 days of gestation but is not completed until long after birth (Lyne & Hollis 1973). The tissue which goes on to develop into the horn bud is ectodermal in origin, with the inner layers of the skin of the bud producing specialised dermal papillae from which horn subsequently grows. It is interesting that the horn bud is the only body area in cattle where hair follicles, sweat glands and sebaceous glands initially grow and then subsequently degenerate. Degeneration of these structures commences when the horny sheath starts to thicken. While the horny sheath of the horn is composed of dense keratin, it is suggested that its structure resembles that of modified hair (Lyne & Hollis 1973). The summary seems to be that the epidermis of the horn bud area initially differentiates as normal epidermal tissue during the first trimester of gestation, with hair follicles, sweat glands and sebaceous glands. However, during the second trimester of gestation in horned animals, this area re-differentiates into tissue capable of producing horn. The inference is that the presence of the poll gene prevents the gene-switching events necessary for this re-differentiation of the epidermal tissue to occur. One interesting finding identified in a study on sheep was the fact that epidermal re-differentiation into horn-producing tissue seemed to involve the development of a connective tissue sheath around the base of groups of primary hair follicles (Lyne & Hollis 1973). This does not occur in polled animals.

The poll gene is located on chromosome 1 in *Bos taurus* breeds. While the exact location of the gene is yet to be determined it is considered to be close to the centromere (Prayaga 2007). The only association between the polled condition and functional reproductive anatomy or physiology in cattle, which has strong scientific evidence, is the negative influence it has on the development of the striated caudal preputial muscle (Bruner & Van Camp 1992; Long & Hignett 1970; Rice 1987). There is evidence that small, or absent caudal preputial muscles are associated with an increased prevalence of preputial eversion as described in Section 3.5.2.

When looking for a link between polledness and bovine penile dysfunction, it seems that most problems of bovine erection and ejaculation relate to pathological, anatomical and developmental problems of fibrous and vascular structures rather than the physiological control of smooth or striated muscle (Ashdown 2006). This suggests that if the poll gene is to influence the prevalence of PSDP, it would most likely be through mechanisms which have not yet been identified. These mechanisms would most likely have to influence the development of the dorsal apical ligament of the penis. It seems that until the exact mechanism by which the poll gene prevents epidermal re-differentiation of the horn bud is identified, it will be difficult to relate its presence to penile dysfunction or infertility in the bull.

An interesting, yet unproven concept that may produce an indirect influence on fertility is that the high vascularity of horns may assist with thermoregulation in the male (Lyne & Hollis 1973). Thus, there is the possibility that in conditions of high environmental temperatures, horned bulls may have greater thermoregulatory capacity than polled bulls. While it seems intuitive that the core temperature difference between horned and polled animals would be minimal, it would still

be valuable to perform a controlled study to quantify any differences. Such information may allow more accurate recommendations to be made on the suitability of polled animals for different environments.

4.7.1 The relationship of the poll gene to male infertility in other species

Abnormal sexual differentiation leading to intersex is relatively common in polled dairy breed goats. It is hypothesised that in goats, the intersex and polled traits are linked, meaning that they are controlled by genes which are on closely apposed loci on the same chromosome (Mickelsen & Memon 2007). Most intersex cases in polled goats are male pseudohermaphrodites. This means that the gonads are testicles and the external genitalia variable, but tending towards female phenotype. Karyotypically, male pseudohermaphrodite cases are XX females. Therefore, this manifestation of poll gene-linked infertility is not relevant to cattle.

Recent studies have shown that the gene for polledness in goats is located on the long arm of chromosome 1 at the band designated as 1q43 (Vaiman 2000). This can be compared to cattle where the poll gene has also been mapped to chromosome 1 (Georges *et al.* 1993). Further studies in goats have narrowed the location of the mutation responsible for the polled trait-related intersex syndrome (PIS) to a small deletion of DNA which has long-range regulatory effects on two important genes involved in horn bud development and gonadogenesis (Pailhoux, Vigier, & Chaffaux 2001). An important polled trait-linked problem in polled bucks (XYPP) that may be relevant to cattle is sterility associated with poor differentiation of the androgen dependent duct system (Basrur & Kochhar 2007). Thus there is a precedent for the poll gene adversely affecting the development of the testicular efferent duct system which may be worthy of exploring further in bulls.

In sheep, there seems to be less influence of the polled condition on fertility compared to goats. For example, the reproductive efficiency of 64 polled Merinos rams was compared to that of 68 horned Merinos (Dun & Douglass 1965). The study measured lambing percentages over several joining periods and found no difference between the reproductive performance of the polled ram or horned ram flocks.

4.8 An exploration of the potential effect of the poll gene on a selection of heritable causes of infertility in the bull

Diplomates of the American College of Theriogenologists (ACT) were canvassed via the ACT email list-serve for comment or anecdote on any associations they may have made between the poll gene and bull infertility. Most North American large animal reproductive specialists access this list. While there were only five responses to the request for information, the answers most likely reflect the opinions of the College, as previous experience has seen very vigorous debate on issues of contention. The responses all suggested there may be an increase in preputial prolapse in polled bulls and one response suggested the possibility of an association with PSDP. No diplomates had, or were willing to produce, original data to substantiate their views. There was no data or anecdote suggesting there were any other potential negative implications of the poll gene on bull fertility.

The literature was reviewed to identify causes of infertility in the bull that are either known to be heritable, or for which there is strong circumstantial evidence that they are heritable. Data for the literature review was collected from a number of sources (Madrid *et al.* 1988; Steffen 1997; Van Camp 1997) and is presented in .

It should be noted that for many of the listed abnormalities there are a number of causes, of which a genetic cause is just one. Once the list was generated, the literature was reviewed to determine if there was any known, suspected, or theoretical relationship between specific abnormalities and the poll gene. For the abnormalities listed in , no association with the poll

Breeding Soundness Abnormalities in Polled and Horned Bulls

gene was described in the literature or anecdotally. However, by extrapolating information from the goat, there is a theoretical mechanism whereby the poll gene could be associated with efferent duct obstruction and sperm stasis, and subsequent testicular enlargement and degeneration or spermatic granuloma of the head of the epididymis. Until the mechanism of action of the poll gene in cattle is understood then this theoretical association cannot either be ruled out or confirmed.

Table 2 – Some causes of infertility in the bull that may be heritable, for which there is no evidence of a real or theoretical relationship to the poll gene. Note that the reference only refers to the source of heritability information, it does not refer to any research into the poll gene.

Cause of Infertility	Classification	Reference
Hypothalamic/Pituitary dysfunction	H	(Van Camp 1997)
Autoimmunity	H	(Van Camp 1997)
Chromosomal aberrations	H	(Van Camp 1997)
Freemartin co-twin	H	(Van Camp 1997)
Pampiniform phlebitis/varicocele	H	(Van Camp 1997)
Inguinal hernias	H	(Van Camp 1997)
Cryptorchidism	H, C	(Van Camp 1997)
Scrotal fat	H	(Van Camp 1997)
Duct obstruction/sperm stasis	H	(Van Camp 1997)
Testicular hypoplasia	H	(Madrid, Ott, Rao Veeramachaneni, Parrett, Vanderwert, & Willms 1988)

H = heritable, C = congenital

4.9 A note on persistent frenulum

The frenulum is a thin band of connective tissue joining the urethral surface of the collum glandis penis to the penile prepuce, extending from the base of the collum glandis to the base of the urethral process. It is most likely of ectodermal origin (Ashdown 2006). Progressive epithelial separation of the prepuce from the penis occurs between four to nine months of age. During this time the frenulum ruptures and this rupture line remains as an obvious raphe on the ventral penis and a less-obvious raphe on the prepuce. Near the most distal extremity of the raphe penis there frequently remains a flap of tissue in the normal adult penis. The frenulum seems especially resistant to rupture at this point. A vein from the csp may traverse the foetal/postnatal frenulum at this point to join the ventral vein of the prepuce (Ashdown 1962).

When part or all of the frenulum fails to rupture after attaining puberty, intromission for natural service is usually impossible. If intromission is attempted, the erect collum glandis penis is bent ventrally into a hooked shape (Ashdown 2006).

Four reports were identified that had data on the prevalence of persistent frenulum (Bertram 1999; Carroll, Aanes, & Ball 1964; Carroll, Ball, & Scott 1963; Spitzer *et al.* 1988). Carroll *et al.* (1963) reported a prevalence of 0.5% in 10,940 BBSE examinations. While no statistical analysis was presented, these authors claimed most of the cases were in Shorthorn cattle or polled breeds, and they suggested the condition may be heritable. Spitzer *et al.* (1998) reported a prevalence of less than 2% in a mixed population including 359 Angus, 107 Santa Gertrudis, 107 Simmental and 99 Poll Hereford bulls, while Bertram (year???) reported a prevalence of 1.6% in 558 Santa Gertrudis bulls.

Breeding Soundness Abnormalities in Polled and Horned Bulls

Based on these studies and contemporary industry anecdote, the conclusions that can be drawn are that the prevalence of persistent frenulum is quite low. There is little evidence it is associated with the polled condition. Consistent with the hypothesis that the poll gene may adversely affect connective tissue development, there is a small theoretical possibility it may be linked with the polled condition. However, the fact that persistent frenulum can be readily detected at a young age during routine bull breeding soundness evaluations allows affected bulls to be readily removed from the gene pool. This makes it a low risk problem even if an association with the poll gene was proven.

5 Part 1 – Survey of contemporary industry BBSE data

A large amount of the initially collected data was rejected due to deficiencies in critical components, e.g. identification of breed and age of the bulls. Initially the data was collated by the veterinary practice/researcher that provided the data, but it was then subsequently pooled for analysis. The most commonly reported penile abnormality was PSPD. Other abnormalities reported were retained frenulum, spiral deviation of the penis during electro ejaculation and ventral deviation of the penis, penile haematoma, preputial damage and penile adhesions. PSPD was recorded in *Bos taurus* (including tropically adapted Sanga breeds) and *Bos indicus* breed bulls. Any differences in reported prevalence of PSPD across the reporting sites appeared to be mainly a reflection of the age of the bulls tested and the primary purpose of the BBSE conducted.

As would be expected, the results indicate that generally few bulls are observed with penile abnormalities at one and two years of age (0% and 0.9% overall prevalence, respectively). The prevalence of PSDP by breed in three to six-year old bulls ranged from 0% to 30% with an average of 8.2% across all breeds (). It would be inaccurate to make conclusions about breed predisposition because of small sample size (<25) for some breeds (Table 2). However, the reported prevalence of PSDP was markedly higher in three to six year old bulls, with 12.6% prevalence in polled-breed bulls, 3.7% in horned-breed bulls and 6.3% in mixed horn status breed bulls (). Bulls reported to be six years and older had an increased prevalence of PSDP with 18.4% and 14.0% of Polled- and Horned-breed bulls, respectively exhibiting PSDP. Further 21.7% of greater than six year old mixed horn status-breed bulls showed signs of PSDP. The pooled data across all age groups (see Table 2) showed that 4.4% of Polled-breed bulls (n=2431), 1.5% of Horned-breed bulls (n=1433) and 3.4% of mixed horn status- breed bulls (n=2173) were diagnosed with the PSDP condition.

Table 3 - Veterinary practice/research database survey of prevalence of PSPD in beef bulls in Australia by breed and age

Breed	No.	Age	PSPD
Crossbreds	3	1 yr old	0.00%
Poll Shorthorn	7	1 yr old	0.00%
Angus	18	1 yr old	0.00%
Murray Grey	4	1 yr old	0.00%
Belmont Red	201	1 yr old	0.00%
Braford	11	1 yr old	0.00%
Gelbvieh	1	1.5 yr old	0.00%

Breeding Soundness Abnormalities in Polled and Horned Bulls

Total 1 yr old	245		0
Crossbreds	5	2 yr old	0.00%
Santa x Angus	14	2 yr old	0.00%
Poll Shorthorn	35	2 yr old	5.71%
Angus	236	2 yr old	0.42%
Murray Grey	69	2 yr old	0.00%
Char x MGrey	3	2 yr old	0.00%
Poll Hereford	381	2 yr old	1.05%
Hereford	351	2 yr old	0.85%
Wagyu	6	2 yr old	0.00%
Red Poll	4	2 yr old	0.00%
Simmental	5	2 yr old	0.00%
Limousin	32	2 yr old	12.50%
Gelbvieh	1	2 yr old	0.00%
Belmont Red	51	2 yr old	0.00%
Santa Gertrudis	501	2 yr old	0.40%
Total 2 yr old	1694		0.9% (16)

Breeding Soundness Abnormalities in Polled and Horned Bulls

Table 3 (cont.)

Crossbreds	3	3-6 yr old	0.00%
Poll Hereford	63	3-6 yr old	6.34%
Hereford	183	3-6 yr old	3.83%
Angus	221	3-6 yr old	12.67%
Red Angus	4	3-6 yr old	0.00%
Beef Maker	4	3-6 yr old	0.00%
Red Poll	10	3-6 yr old	30.00%
Shorthorn	9	3-6 yr old	0.00%
Poll Shorthorn	80	3-6 yr old	17.50%
Wagyu	40	3-6 yr old	0.00%
Murray Grey	86	3-6 yr old	18.60%
Char x MGrey	24	3-6 yr old	4.17%
Limousin	46	3-6 yr old	2.17%
Charolais	1	3-6 yr old	0.00%
Gelbvieh	5	3-6 yr old	0.00%
Simmental	23	3-6 yr old	0.00%
Belmont Red	28	3-6 yr old	10.71%
Santa Gertrudis	109	3-6 yr old	0.00%
Total 3-6 yr old	939		8.2% (77)
Angus	40	6+ yr old	15.00%
Murray Grey	17	6+ yr old	29.41%
Poll Hereford	4	6+ yr old	0.00%
Poll Shorthorn	29	6+ yr old	20.69%
Red Poll	3	6+ yr old	66.66%
Hereford	43	6+ yr old	13.95%
Simmental	3	6+ yr old	0.00%
Limousin	37	6+ yr old	21.62%
Santa Gertrudis	3	6+ yr old	0.00%
Total 6+ yr old	179		18.4% (33)

Breeding Soundness Abnormalities in Polled and Horned Bulls

Table 3 (cont.)

Poll Hereford	466	AE*	0.00%
Hereford	373	AE*	0.00%
Angus	385	AE*	0.00%
Shorthorn	46	AE*	0.00%
Wagyu	106	AE*	0.00%
Murray Grey	69	AE*	0.00%
Devon	65	AE*	0.00%
Limousin	73	AE*	0.00%
Charolais	22	AE*	0.00%
Simmental	154	AE*	0.00%
Shaver	3	AE*	0.00%
Mandalong Special	29	AE*	0.00%
Braford	22	AE*	0.00%
Santa Gertrudis	104	AE*	0.00%
Angus	350	ANR**	9.14%
Poll Hereford	2	ANR**	50.00%
Murray Grey	24	ANR**	4.17%
Crossbreds	5	ANR**	80.00%
Hereford	331	ANR**	0.60%
Shorthorn	140	ANR**	6.45%
Char x MGrey	91	ANR**	12.09%
Limousin	47	ANR**	21.28%
Charolais	49	ANR**	0.00%
Gelbvieh	24	ANR**	0.00%
Total unknown age bulls	2980		2.4% (73)
Total all bulls	6037		3.3% (199)
AE* - age estimated by vet to be mostly < 4yr old			
ANR** - age not recorded – no estimate of age available			

Breeding Soundness Abnormalities in Polled and Horned Bulls

Table 4 - Summary of veterinary practice/research database survey of prevalence of PSPD in beef bulls in Australia by breed-horn status

Breed*	Age	No. Poll Breed	No. Horn Breed	No. Mixed Horn	PSPD
Poll Shorthorn, Angus	1 yr old	25			0% (0)
Braford	1 yr old		11		0% (0)
Crossbreds, Murray Grey, Belmont Red, Gelvbieh	1 yr old			209	0% (0)
Poll Hereford / Shorthorn, Red Poll, Angus, Red Angus, Murray Grey	2 yr old	707			0.99% (7)
Hereford, Limousin*, Wagyu	2 yr old		379		1.85% (7)
Crossbreds, Santa x Angus, Wagyu, Simmental Limousin, Gelvbieh, Belmont Red, Santa Gertrudis, Charolais x Murray Grey, Murray Grey	2 yr old			602	0.33% (2)
Poll Hereford / Shorthorn, Red Poll, Angus and Red Angus, Murray Grey, Limousin	3-6 yr old	420			12.62% (53)
Hereford, Limousin	3-6 yr old		190		3.68% (7)
Crossbreds, Shorthorn, Wagyu, Murray Grey Char x MGrey, Limousin, Charolais Gelbvieh, Simmental, Belmont Red, Santa Gertrudis, Beef Maker	3-6 yr old			335	6.27% (21)
Poll Hereford / Shorthorn, Red Poll, Angus,	6+ yr old	76			18.42% (14)
Hereford	6+ yr old		43		13.95% (6)
Simmental, Limousin, Santa Gertrudis and Murray Grey	6+ yr old			60	21.67% (13)
Poll Hereford, Angus	ANR	1203			2.74% (33)
Hereford, Wagyu	ANR		810		0.25% (2)
Crossbreds, Shorthorn, Wagyu, Murray Grey Char x MGrey, Devon, Limousin, Charolais Gelbvieh, Simmental, Shaver, Mandalong Special, Braford, Santa Gertrudis	ANR			967	3.93% (38)
Totals by breed-horn status across ages		2431			(4.40%)107
			1433		(1.54%) 22
				2173	(3.41%) 74

* where a breed appears in more than one horn status category this is on the basis of confirmed horn status data provided at the time of examination

Breeding Soundness Abnormalities in Polled and Horned Bulls

Table 5 Results of the generalized linear mixed model (GLM) with PSPD as the outcome variable and age and breed-horn status as covariates. Model was developed using STATA Version 9.2 (STATA Corp.)

Variable/Category	Coef.	SE	z	p-value	95%CI	
Horn Status						
<i>Polled</i>	Ref.					
<i>Mixed</i>	-0.06	0.07	-0.94	0.35	-0.19	0.07
<i>Horned</i>	-0.06	0.03	-1.76	0.08	-0.12	0.01
Age						
<i>1-year old</i>	Ref.					
<i>2-year old</i>	0.02	0.05	0.32	0.75	-0.08	0.11
<i>3 – 6 years old</i>	0.06	0.05	1.22	0.22	-0.03	0.15
<i>>6 years old</i>	0.18	0.05	3.35	0.001	0.07	0.28
Intercept	0.04	0.05	0.89	0.37	-0.05	0.13

Statistical modelling of the data demonstrated that there was no significant difference ($P>0.05$) in prevalence of PSPD between polled, horned or mixed horn-status breed bulls, although the difference between polled and horned breed bulls approached statistical significance ($p=0.079$). After controlling for the effect of breed-horn status, increasing age was found to be significantly associated with an increasing prevalence of PSPD, being 17% higher in beef bulls > 6 years of age compared to 1-year old bulls ($p=0.001$).

6. Discussion

Results from Part 1 of this project highlight that the industry impression of the polled condition being associated with a higher prevalence of bull infertility problems is generally based on a very small number of studies and anecdote. Analysis of published data suggests only a tenuous association between some polled breeds and an increased prevalence of some infertility traits. No evidence directly associating the poll **gene** with bull infertility was identified. This finding was supported by results from Part 2 of the project which found that whilst the prevalence of PSDP appears to be greater in some polled breeds, there was no evidence from the data analysed that it is linked to the polled condition or the polled gene, but rather is probably a reflection of the focussed sire selection in those breeds. The converse of this conclusion may be evident in the tropically adapted breeds examined.

While there is no direct evidence that the poll gene is associated with bull infertility, there is a need to understand mechanisms by which it could influence pathological conditions such as PSDP in order to assist with assessing the potential risks associated with widespread dissemination of the poll gene. Three hypotheses on how traits such as PSDP, preputial prolapse and persistent frenulum may be associated with the poll gene are:

1. The poll gene may be pleiotropic, thereby directly influencing traits other than polledness.
2. There may be linking (coupling) of the poll gene with undesirable traits.
3. The poll gene may be associated with negative allele effects on different chromosomes.

The nature of pleiotropy is that one gene can influence a number of phenotypic traits. If the poll gene is pleiotropic then it will be difficult to widely distribute it without also distributing associated traits. If, however, there is coupling of the poll gene with other traits, it is possible that genetic marker technology would help to disassociate undesirable traits from the poll gene.

Breeding Soundness Abnormalities in Polled and Horned Bulls

The breeding history of polled bulls could support a hypothesis of negative allele effects. At the commencement of breeding polled bulls, it is possible that little selection pressure for reproductive traits was applied. Thus, polled breeds are potentially a number of years behind horned breeds in improvement in reproductive traits as there probably was a period in their breed development when there was selection primarily for the polled condition. In this case, it should be possible to substantially reduce, if not eliminate, any undesirable effects of selection for the polled condition.

Published results on the prevalence of PSDP in polled bulls compared to horned bulls suggest that some breeds of polled bull are at a greater risk of developing PSDP. However more recent studies also suggest that there are some breeds/lines of horned bulls that have an increased risk of developing PSDP. Thus, the evidence suggests that PSDP is likely to be heritable, and unlikely to be associated with the poll gene.

Results from investigation into the prevalence of preputial prolapse revealed a very specific link between the polled condition and a reduction, or absence in the caudal preputial muscle. In *Bos taurus* bulls, this appears to be associated with an increased prevalence of preputial eversion, but not preputial prolapse. There is minimal evidence to suggest preputial eversion is associated with increased preputial prolapse in *Bos indicus* derived breeds. Most evidence suggests that sheath structure may have more of an influence on the occurrence of preputial prolapse compared to the presence or absence of the caudal preputial muscle.

The review of the literature failed to identify any evidence for an association between the polled condition and reduced serving capacity. In addition, it was established that a paper published in the early 1980s was most likely incorrectly interpreted, leading to a false perception that these two traits were linked.

Investigation into the prevalence of persistent frenulum failed to identify any evidence of a link with the polled condition. The fact that persistent frenulum occurs at a very low prevalence within the bull population, and it is readily diagnosed at a young age means that it is a low-risk potential problem.

Investigation of the literature for other abnormalities that may be affected by the polled condition only identified one remote possibility. Based on extrapolation from abnormalities in polled goats, it is considered theoretically possible that efferent duct obstruction and subsequent sperm stasis in the testis and head of the epididymis could be influenced by the poll gene. This condition would most likely manifest clinically as progressive testicular enlargement and degeneration or spermatic granuloma.

A major finding from part 2 was that PSPD was by far and away the most common abnormality affecting the serving ability/serving capacity of bulls detected by veterinarians and researchers. This abnormality was rarely detected in young bulls (1- to 2-year olds) but across breeds 8.2% (n=939) of 3- to 6-year old and 18.4% (n=179) of >6-year old bulls were diagnosed with PSPD. For bulls \geq 3-years of age approximately twice as many cases of PSPD were detected in polled-breed bulls (13.5%; n=496) compared to horned-breed bulls (5.6%; n=233), clearly indicating that it is a much greater problem in polled-breed bulls but occurs frequently enough in horned-breed bulls to suggest that it is unlikely to be simply associated with the polled gene.

To summarise, it is of real concern how such a small number of studies have had such a profound influence on industry perceptions. This is particularly so considering the fact that many of the early studies should more correctly be considered anecdote and personal opinion rather than scientific reports. While there are some areas identified in this project that warrant further investigation, the conclusion to be drawn is that the widespread dissemination of poll genetics is unlikely to result in a significant decrease in bull fertility. However, as there have been no

studies which have definitively described the relationship between the polled condition and specific bull breeding soundness abnormalities, and thus it is possible that a genuine relationship does in fact exist, it is recommended that the prevalence of abnormalities such as PSPD be monitored using a similar approach to that used in Part 2 of this project.

7. Success in Achieving Objectives

Achievement against each objective is summarised below.

1. Review of the normal anatomy and physiology of the penis and prepuce of bulls.

The anatomy of the penis and prepuce was reviewed using nomenclature described by the International Committee on Veterinary Gross Anatomical Nomenclature (1994) to standardise nomenclature and to provide a detailed understanding of the structure and function of the penis and prepuce (Section 4.3).

2. Review the pathogenesis of PSDP and preputial prolapse in the bull, particularly focussing on evaluating the evidence of any association between the polled gene and these abnormalities.

PSDP is reviewed in Section 4.4 and preputial prolapse is reviewed in Section 4.5. The only mode of action identified in this review whereby the poll gene may have an influence on the occurrence of PSDP is if it has an influence on the development of the dorsal apical ligament of the penis. There is a theoretical mechanism proposed as to how this may occur. The only scientifically validated influence of the polled condition on preputial anatomy identified by this review is the absence of a caudal preputial muscle in a significant proportion of polled bulls. No scientific evidence was identified which linked the absence of this muscle to an increased prevalence of preputial prolapse in polled *Bos taurus* bulls. However, there was some evidence it may contribute to an increased prevalence of preputial prolapse in polled *Bos indicus* bulls when poor sheath structure is concomitantly present.

3. Identify breeding soundness abnormalities in bulls which have either a known, or strongly suspected genetic aetiology.

Selected abnormalities are listed in Section 4.8. No further associations (scientific or anecdotal) of the poll gene to bull infertility in the bull were identified. One theoretical association involving the testicular efferent duct system was identified by extrapolation from literature on the buck goat. Specific reference was made to the condition of persistent frenulum in Section 4.9. No further associations (scientific or anecdotal) of the poll gene to bull infertility in the bull were identified.

4. Identify heritable abnormalities known to affect the fertility of males in other species.

The influence of the poll gene on fertility in other species is reviewed in Section 4.6. One theoretical association was identified by extrapolation from literature on the buck goat

5. Estimate the prevalence of PSDP and other penile abnormalities in a selected population of polled and horned breed beef bulls in Australia.

Data on some 6,200 bulls was collated. Results from this survey supported findings from Part 1 that there is no evidence PSDP is associated with the polled gene.

6 Provide recommendations to industry on how to minimise the risk of adversely affecting bull breeding soundness by selecting for the polled condition.

Industry recommendations are presented in section 9.

8 Impact of the poll gene on bull fertility – now & in five years time

8.1 Impact of the poll gene on bull fertility – Now

Currently, there is some conflicting scientific and anecdotal evidence as to the impact the poll gene may be having on bull fertility. Much of the scientific evidence is now quite old, and when interrogated, commonly found to be based on unsubstantiated anecdote which has been repeatedly referenced in subsequent literature. The only three pieces of scientific evidence that could be identified relating to the influence of the polled condition on bull fertility were:

1. The polled condition is associated with a reduction in size, or the absence of, the caudal preputial muscle.
2. Reduction in the size of the caudal preputial muscle is associated with an increased prevalence of preputial eversion.
3. More than 20 years ago a high prevalence of PSDP was recorded in a highly selected population (veterinary referral cases) of polled breed bulls. However, this finding is countered by contemporary studies which have identified cohorts of horned bulls with a high prevalence of PSDP.

Other than these three facts, there appears to be only older anecdotal evidence of an increased prevalence of conditions such as preputial prolapse in polled bulls. More contemporary anecdote suggests that the current impact of the poll gene on bull fertility is minimal, with factors (such as pendulous sheath and ventral-facing sheath opening) apparently unrelated to the polled condition, having more influence on the reasons for bull breakdown. Thus, it can be stated with reasonable confidence that the poll gene is currently having minimal negative impact on bull fertility or breeding soundness.

8.2 Impact of the poll gene on bull fertility – Five years time

The value of large-scale dissemination of the polled condition throughout the beef-cattle industry is immense. Not only from the direct animal welfare point-of-view, but also from the economic value of being able to market a product that is more acceptable to export markets and the end consumer based on current and likely future concerns about animal welfare. Reducing, or eliminating the need to dehorn cattle will also have immense cost savings due to reducing the time and labour necessary to carry out this surgical husbandry procedure.

Increasing the prevalence of the poll gene throughout the beef industry is a highly desirable goal. It is recommended that any large-scale dissemination of the polled condition be in conjunction with an integrated programme of monitoring, research and extension. As with any major innovation, close monitoring of bull fertility and production traits will be necessary during the roll-out period. The dominant poll gene has been described as a mutant (Prayaga 2007). As such, it would be unreasonable to expect that it only influenced one very discrete phenotypic outcome. This has been explored in relation to production traits in cattle (Lamminger, Hamann,

Breeding Soundness Abnormalities in Polled and Horned Bulls

Rohrmoser, Rosenberger, Krausslich, & Distl 2000). Possible “worse-case” scenarios regarding the wide-spread dissemination of the poll gene and bull fertility are that:

1. It may be found that preputial eversion does predispose to preputial prolapse.
2. The poll gene (in contrast to some polled breeds) is linked to PSDP
3. The poll gene is linked to abnormal development of the efferent duct system within the testes.
4. The poll gene is linked to an increased prevalence of persistent frenulum.

In addressing these possibilities sequentially:

Preputial eversion has been demonstrated to be highly heritable. There has also been a relatively simple observation test described which can be used on young bulls as a selection tool. Thus, it is suggested that even if preputial eversion were found to be undesirable, it could be readily selected against.

It seems highly unlikely that the poll gene is directly associated with increased prevalence of PSDP. This is based on recent studies identifying high PSDP prevalences in horned bulls and results from Part 2 of this project. It is also unlikely that the poll gene would be pleiotropic with respect to PSDP based on reports failing to find occurrences of PSDP in proportions consistent with the phenotypic outcomes anticipated if such pleiotropy were present. Thus, if there was a relationship between the poll gene and PSDP, it would more likely be due to coupling or via a negative allele effect. In both of these latter instances, the negative effect can be disassociated from the positive effect by using selection tools such as marker technology. In this regard, focussing research attention on the development of an early test for PSDP would be advantageous.

An association between the poll gene and the efferent duct system of the testes is only a theoretical possibility. If it were found to be true, the same argument made for PSDP above could be made in that disassociation of the negative effect from the positive effect should be possible.

With regard to persistent frenulum, the prevalence of this problem is so small that it will have minimal impact on the beef industry. The other positive aspect in the control of this condition is that it is relatively easy to diagnose in young bulls. This means that bulls with this condition can be readily removed from the breeding herd before passing on their genetics.

Over the next five years, it is anticipated that an increased prevalence of the polled condition would have no or minimal negative influence on bull fertility. It is envisioned that with an increased roll-out of the poll gene into the beef cattle industry, there will be an accompanying programme of monitoring, research and extension to ensure a deeper understanding of the action of the poll gene is gained and that no untoward conditions develop. In particular, it is recommended that known influences of the polled condition (reduced caudal preputial muscle and preputial eversion) are investigated to ensure they do not have significant negative influences on production traits of progeny. An example of where research could be focussed is to investigate whether preputial prolapse in feedlot steers is related to preputial eversion in polled bulls.

9 Conclusions and Recommendations

presents a summary of prevalences of breeding soundness abnormalities that have been reported to be apparently associated with the polled condition. For PSDP, the prevalences listed at the top of the column are estimated mean ranges based on the multiple reference sources. All other figures are as quoted in the accompanying reference.

Table 5 Summary of estimates of prevalences of conditions reviewed in this report. Note that preputial eversion is not considered a pathological condition, but is included as some authors have associated it with preputial prolapse.

Condition	Polled Breeds	Horned Breeds	All Breeds	Reference
PSDP	10% to 16% Maximum 27%	1% to 13.5% Maximum 26%	2% to 14% Maximum 27%	(Bertram 1999; Blockey & Taylor 1984; Carroll, Ball, & Scott 1963; McDiarmid 1981)
Preputial Eversion	81%	64%	74%	(Long & Dubra 1972)
Persistent Frenulum	No data	No data.	0.5%	(Carroll, Ball, & Scott 1963)

Information on the effect of the poll gene on bull fertility appears to be substantially influenced by industry anecdote and dogma. It seems that concern regarding a possible reduction in serving capacity associated with the polled condition may have originated from an erroneous interpretation of one Australian study (Blockey & Taylor 1984). Thorough review of the available English and German literature, failed to identify any evidence to suggest that the polled condition is related to reduced serving capacity.

In the case of PSDP, it appears that the concern regarding the adverse influence of the polled condition is based on a small number of papers, only one of which has the required sample size and statistical rigour. Evidence of an association between PSDP and the polled condition is generally based on poorly controlled studies with relatively small numbers of animals. This is a common problem associated with investigating such traits in a commercial environment. A large Australian study is the exception. Despite these problems, there is tenuous scientific evidence that the polled condition may have been linked to an increased prevalence of PSDP 20 to 50 years ago. Significantly, examination of the data in these studies identified that prevalence of PSDP was more likely associated with breed and familial lines, in contrast to a specific association with the poll gene. Subsequent authors referring to these studies have perhaps erroneously concluded that perceived increases in prevalences of PSDP in polled breeds implies a direct association with the poll gene. This may not be the case and is a very important distinction to make as the former situation would allow marker assisted selection to effectively address antagonistic genetic associations.

One member of the Australian Cattle Veterinarians, who has performed thousands of serving capacity tests on *Bos taurus* breeds (mainly Angus, Hereford, Polled Hereford and Murray Grey) claims that it is unusual to find more than two percent PSDP in any group of bulls that he examines (R Holmes *pers. comm.*). This is similar to the prevalence reported by other authors (Carroll, Ball, & Scott 1963). Holmes (*pers. comm.*) finds the prevalence of PSDP described in the Australian study (Blockey & Taylor 1984) difficult to comprehend and suggests that if PSDP prevalence of greater than 10% really was representative of the polled breeds at that time, then increased serving capacity testing and genetic selection over the last 23 years must have significantly reduced it to the low prevalence he is currently observing. This could be consistent

Breeding Soundness Abnormalities in Polled and Horned Bulls

with the poll gene having a negative allele effect on other chromosomes, with those negative effects being progressively selected against.

Additionally, impressions from canvassing diplomates of the American College of Theriogenologists suggested that they did not consider PSDP a major concern in polled bulls compared to horned bulls. This is not to say that the two traits are not linked, but more that they considered the advantages of the polled condition outweigh the disadvantages associated with PSDP.

There is still conjecture as to whether PSDP is a heritable or congenital abnormality. However, there are two significant contemporary studies which suggest PSDP is heritable and not related to the polled condition (Bertram 1999; Bertram, Smith, & Foote 1993). These two studies identified a high prevalence of PSDP in horned bulls and throw significant doubt on the validity of earlier studies which implicated a relationship between PSDP and the polled condition. These latter two studies add significant weight to the possibility that PSDP is a heritable condition unrelated to the poll gene and are supported by results from Part 2 of this project.

There is a theoretical possibility that the poll gene, or a DNA fragment influenced by the poll gene, could modify the structure or function of the dorsal apical ligament of the penis. It will be difficult to investigate this further prior to the exact location of the poll gene being identified on chromosome 1, identification of its mode of action to prevent horn bud development, and any DNA deletions or influences that may be associated with its presence. This is an area where research could be focussed.

From this project, it appears that there is no evidence that PSDP is directly associated with the polled condition. One approach to determining whether PSDP is associated with the poll gene, or polled breeds has not been used, is to investigate the prevalence of PSDP in polled breeds that have developed independently to the traditional Angus and Polled Hereford breeds. One such example might be the Senepol breed, which was developed in the Caribbean in the early 1900s. While the Senepol breed does include Red Poll genetics, the N'Dama stock adds a significant degree of genetic diversity compared to traditional *Bos taurus* breeds. If a high prevalence of PSDP was found in this breed (for example, in the range of 10% to 16%), it would provide more evidence that the condition was closely associated with the poll gene. However, if the prevalence was found to be low, it would suggest that PSDP is associated with specific breeds rather than the poll gene.

With regard to preputial prolapse, there is some scientific evidence to suggest that preputial prolapse may be influenced more by sheath structure (pendulousness and angle of sheath opening) than any factors specifically related to the polled condition. While the polled condition has been associated with an increased prevalence of preputial eversion, there is no evidence that preputial eversion is associated with an increased prevalence of preputial prolapse in *Bos taurus* breeds. However, further research on the influence of preputial eversion in *Bos indicus* derived breeds is warranted as there is some evidence suggesting that preputial eversion in conjunction with poor sheath structure may predispose to preputial prolapse. Finally further research is recommended to investigate the influence that a bull which repeatedly everts its prepuce has on its steer progeny. In particular, whether the steer offspring of these bulls have an increased risk of preputial prolapse in the feedlot situation.

9.1 Specific conclusions from the systematic review (Part 1)

1. There is very little scientific evidence to support a direct association between the poll **gene** and abnormalities affecting bull breeding soundness.
2. There may be some breed predispositions to abnormalities such as PSPD. Information from more than 20 years ago suggests a higher representation of some polled **breeds** showing PSDP.
3. PSDP appears to be a heritable condition most commonly identified in older bulls. As such it has the potential to be insidiously maintained within the breeding population unless effective methods of early detection of this abnormality can be identified.
4. The poll gene is not associated with reduced serving capacity or libido.
5. It is necessary to understand the relationships between the poll gene and fertility traits (be that pleiotropic, coupled, negative allele effects, or other) in order to accurately estimate the risks associated with widespread dissemination of this gene.
6. There is some scientific evidence which indicates that the perceived negative effects of the polled condition may be effectively selected against using conventional methods of genetic selection. In particular, the increased prevalence of preputial eversion in polled bulls could be reduced with the use of relatively simple observational tests as described by Lagos and Fitzhugh (1970).
7. The overall assessment, taking into account contemporary industry anecdote is that the benefits of increasing the frequency of the poll gene significantly outweighs its potential negative influence on bull fertility.

9.2 Specific conclusions from the retrospective analysis of BBSE data (Part 2)

The most commonly reported abnormality affecting the mating ability/serving capacity of beef bulls was PSPD. The prevalence of this abnormality increased markedly with age, with it rarely been detected in one and two-year old bulls. The overall prevalence of PSPD in polled-breed bulls tended to be greater albeit not statistically significant ($P = 0.079$) than in horned-breed bulls. With the likely greater use of polled-breed bulls in beef herds, producers of polled-breed bulls should be encouraged to conduct serving capacity tests on their ≥ 3 -year old bulls to identify those affected with PSPD, and with the support of relevant breed societies and geneticists strategies should be established to enable seedstock producers to select against this problem.

9.3 Suggested areas for further research

Possible areas for future research identified by this project include:

1. The development of methods for the early detection of PSDP. The ideal test would detect bulls with PSDP at or before 24 months of age and in its final form would either be a blood or tissue test for a DNA marker, or a relatively simple intervention such as the application of a mild electrical stimulus to the penis or pudendal nerves. It is envisaged that initial investigations would focus on the degree of development of the dorsal apical ligament in cohorts of bulls followed by a longitudinal study to monitor the development of PSDP by more conventional natural service tests.
2. Investigation into the prevalence of PSDP in polled breeds which have been developed independent (e.g. Senepol) of the traditional polled breeds of cattle.

Breeding Soundness Abnormalities in Polled and Horned Bulls

3. Investigation into whether preputial eversion in bulls is linked to preputial eversion in their steer progeny. This could be an observational study using techniques similar to those described by Lagos and Fitzhugh (1970) followed by the calculation of its heritability.
4. Investigation into whether preputial prolapse in feedlot steers is related to the sires horn status. Interactions with hormonal growth promotant treatment could also be investigated.
5. Investigation into whether preputial eversion plays a role in thermoregulation in the bull. Outcomes from a study such as this may influence whether future selection pressure is directed at reducing the prevalence of preputial eversion and improving sheath structure, or directed at only improving sheath structure and maintaining the current prevalence of preputial eversion.
6. Investigation into whether preputial eversion is related to preputial prolapse in *Bos indicus* derived breeds.
7. Investigation into whether the horn status influences thermoregulation in the bull.
8. Investigation into whether the polled condition is associated with an increased prevalence of testicular degeneration or abnormalities of the efferent duct system.

In prioritising steps to progress the widespread dissemination of the poll gene throughout the beef industry there are some key points to consider.

1. While acknowledging there is incomplete information on the effects of the poll gene on bull fertility, there seems to be a body of evidence from this review and that of Prayaga (2005) to suggest that the advantages of disseminating the poll gene outweigh any potential disadvantages. With this in mind, it is suggested that there should be no impediment to the stepwise roll-out of widespread dissemination of the poll gene from the perspective of bull fertility.
2. During the roll-out of the poll gene, extension to industry of the value of sound sheath structure and description of the technique for selecting sound sheath structure should be a high priority, particularly in *Bos indicus* breeds. Sheath selection criteria are outlined by BreedPlan, or in Holroyd *et al* (2000).
3. While not directly related to bull fertility, points 3, 4 and 5 described above should be investigated to determine if there is any potential for the poll gene to influence the prevalence of preputial prolapse in feedlot steers.
4. Investigation into the exact location of the poll gene should be ongoing. There should be concomitant research into the nature of the relationship the poll gene has with other traits.
5. Regardless of any association with the poll gene, the development of a test for the early detection of PSDP is seen as desirable.

10 Glossary

Gene Coupling – Genes are on the same chromosome

Epistatic – Genes may be on the same or different chromosomes. An epistatic gene influences the expression of the gene of interest.

PSDP – Premature spiral deviation of the penis

Pleiotropic - One gene can influence a number of phenotypic traits

Prepuce – The pink, hairless skin contained within the sheath and surrounding the penis

Preputial eversion - A variable length of normal prepuce protrudes temporarily from the preputial orifice which can be voluntarily and readily retracted back into the sheath by the bull.

Preputial prolapse - A variable length of pathologically (swelling or trauma) affected prepuce protrudes from the preputial orifice and is unable to be voluntarily retracted within the sheath.

Sheath – The hair-covered skin running forward from just in front of the scrotum to the umbilicus. The prepuce is contained within the sheath.

11 Bibliography

Aehnelt, E. 1951, "Praputialschlauch und praputialvorfall beim bullen, Deutsches tierärztliche Wochenschrift", *Fortpflanzung und Besamung der Haustiere*, vol. 58, pp. 37-38.

Ashdown, R. R. 1962, "Persistence of the penile frenulum in young bulls", *Veterinary Record*, vol. 74, pp. 1464-1468.

Ashdown, R. R. 2006, "Functional, developmental and clinical anatomy of the bovine penis and prepuce", *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, vol. 1, no. 021, p. 29.

Ashdown, R. R. & Gilanpour, H. 1974, "Venous drainage of the corpus cavernosum penis in impotent and normal bulls", *Journal of Anatomy*, vol. 117, no. 1, pp. 159-170.

Ashdown, R. R., Gilanpour, H., David, J. S. E., & Gibbs, C. 1979, "Impotence in the bull II. Occlusion of the longitudinal canals of the corpus cavernosum penis", *Veterinary Record*, vol. 104, pp. 598-603.

Ashdown, R. R. & Majeed, Z. Z. 1976, "The shape of the free end of the bovine penis during erection and protrusion", *Veterinary Record*, vol. 99, no. 18, pp. 354-356.

Ashdown, R. R. & Pearson, H. 1971, "The functional significance of the dorsal apical ligament of the bovine penis", *Research in Veterinary Science*, vol. 12, no. 2, pp. 183-184.

Ashdown, R. R. & Pearson, H. 1973a, "Anatomical and experimental studies on eversion of the sheath and protrusion of the penis in the bull", *Research in Veterinary Science*, vol. 15, no. 1, pp. 13-24.

Ashdown, R. R. & Pearson, H. 1973b, "Studies on 'corkscrew penis' in the bull", *Veterinary Record*, vol. 93, no. 2, pp. 30-35.

Ashdown, R. R. & Smith, J. A. 1969, "The anatomy of the corpus cavernosum penis of the bull and its relationship to spiral deviation of the penis", *Journal of Anatomy*, vol. 104, no. 1, pp. 153-160.

Australian Meat & Livestock Corporation 1989, *Handbook of Australian Livestock*, 3rd edn, Australian Meat & Livestock Corporation.

Basrur, P. K. & Kochhar, H. S. 2007, "Inherited sex abnormalities in goats," in *Current Therapy in Large Animal Theriogenology*, 2nd edn, R. S. Youngquist & W. R. Threlfall, eds., Elsevier, St. Louis, Missouri, pp. 590-594.

Beckett, S. D., Hudson, R. S., & Walker, D. F. 1978, "Effect of local anesthesia of the penis and dorsal penile neurectomy on the mating ability of bulls", *Journal of the American Veterinary Medical Association*, vol. 173, no. 7, pp. 838-839.

Beckett, S. D., Reynolds, T. M., Walker, D. F., Hudson, R. S., & Purohit, R. C. 1974a, "Experimentally induced rupture of corpus cavernosum penis of the bull", *American Journal of Veterinary Research*.

Breeding Soundness Abnormalities in Polled and Horned Bulls

Beckett, S. D., Walker, D. F., Hudson, R. S., Reynolds, T. M., & Vachon, R. I. 1974b, "Corpus cavernosum penis pressure and penile muscle activity in the bull during coitus", *American Journal of Veterinary Research*, vol. 35, no. 6, pp. 761-767.

Bellenger, C. R. 1971, "Bull wastage in beef cattle", *Australian Veterinary Journal*, vol. 47, pp. 83-90.

Bertram, J. D. 1999, *Structural and behavioural characteristics of reproductive performance in tropically adapted bulls*, Master of Rural Science, The University of New England.

Bertram, J. D., Smith, T., & Foote, T. 1993 "A survey of fertility related conditions encountered in bulls by two veterinary practices in southern Queensland", *Bull Fertility - Proceedings of a Workshop at Rockhampton 8-9 September 1992* R. G. Holroyd, ed., Queensland Department of Primary Industries, Brisbane Qld, pp. 22-25.

Blockey, M. A. d. & Taylor, E. G. 1984, "Observations on spiral deviation of the penis in beef bulls.", *Australian Veterinary Journal*, vol. 61, no. 5, pp. 141-145.

Brandt, K. 1928, "Die Entwicklung des Hornes beim Rinde bis zum Beginn der Pneumatisation des Hornzapfens. 17. Beitrag zum Bau und zur Entwicklung von Hautorganen bei Säugetieren", *Gegenbaurs Morph Jb*, vol. 60, pp. 428-468.

Bruner, K. A. & Van Camp, S. D. 1992, "Assessment of the reproductive system of the male ruminant.", *Veterinary Clinics of North America. Food Animal Practice*, vol. 8, pp. 331-345.

Carroll, E. J., Aanes, W. A., & Ball, L. 1964, "Persistent penile frenulum in bulls.", *J.Am.Vet.Med.Assoc.*, vol. 144, pp. 747-749.

Carroll, E. J., Ball, L., & Scott, J. A. 1963, "Breeding soundness in bulls - A summary of 10,940 examinations", *J.Am.Vet.Med.Assoc.*, vol. 142, pp. 1105-1111.

Cottrell, D. F., Iggo, A., & Kitchell, R. L. 1978, "Electrophysiology of the afferent innervation of the penis of the domestic ram", *Journal of Physiology*, vol. 283, pp. 347-367.

D'Occhio, M. J. & Brooks, D. E. 1983, "Seasonal changes in plasma testosterone concentration Leicester, and mating activity in Border Poll Dorset, Romney and Suffolk rams", *Australian Journal of Experimental Agriculture and Animal Husbandry*, vol. 23, pp. 248-253.

Donaldson, J. E. & Aubrey, J. N. 1960, "Posthitis and prolapse of the prepuce in cattle", *Australian Veterinary Journal*, vol. 36, p. 380.

Entwistle, K & Fordyce, G. 2003, "Evaluating and reporting bull fertility", published by the Australian Cattle Veterinarians, Brisbane, Australia.

Dun, R. B. & Douglass, D. S. 1965, "The comparative reproductive performance of polled and horned Merino rams", *Australian Journal of Experimental Agriculture*, vol. 5, pp. 102-105.

Fournier, G. R., Juenemann, K. P., Lue, T. F., & Tanagho, E. A. 1987, "Mechanisms of venous occlusion during canine penile erection", *Journal of Urology*, vol. 137, pp. 163-167.

Breeding Soundness Abnormalities in Polled and Horned Bulls

Georges, M., Drinkwater, R., King, T., Mishra, A., Moore, S. S., Nielsen, D., Sargent, L. S., Sorensen, A., Steele, M. R., Zhao, X., Womack, J. E., & Hetzel, J. 1993, "Microsatellite mapping of a gene affecting horn development in *Bos taurus*.", *Nature Genetics*, vol. 4, pp. 206-210.

Gilanpour, H. 1972, *Angioarchitecture and Functional Anatomy of the Penis in Ruminants.*, University of London.

Grove, D. 1968, "Andrologische untersuchungen an zeburindern und versuche zur konservierung von rindersamen bei raumtemperaturen," in *Habilitationsschrift*, Tierärztlichen Hochschule, Hannover, Germany.

Holroyd, R.G., Bertram, J.D., Burns, B.M., DeFaveri, J., D'Occhio, M.J., Doogan, V.J., Fitzpatrick, L.A., Fordyce, G., Jayawardhana, G.A., McGowan, M.R., Miller, R.G. 2000, *Bull Selection in Northern Australia. Project : DAQ.104, Final Report.* Queensland Beef Industry Institute, Department of Primary Industries, Qld.

International Committee on Veterinary Gross Anatomical Nomenclature 1994, *Nomina Anatomica Veterinaria*, 4 edn, Zurich, Switzerland.

Izumi, T. 1980, "Neuro-anatomical studies on the mechanism of ejaculatory reflexes in bull", *Bulletin of the Ishikawa College of Agriculture*, vol. 9, pp. 41-85.

Kiss, F. 1921, "Anatomisch-histologische Untersuchungen über die Erektion", *Zeitschrift für Anatomic und Entwicklungsgeschichte*, vol. 61, pp. 455-522.

Lagos, F. & Fitzhugh, H. A. 1970, "Factors influencing preputial prolapse in yearling bulls.", *J.Anim.Sci.*, vol. 30, pp. 949-952.

Lamminger, A., Hamann, H., Rohmoser, G., Rosenberger, E., Krausslich, H., & Distl, O. 2000, "Relationships between polledness and traits used in the breeding objectives for German Fleckvieh", *Zuechtungskunde*, vol. 72, no. 5, pp. 325-339.

Larson, L. L. & Kitchell, R. L. 1958, "Neural mechanisms in sexual behaviour II. Gross neuroanatomical and correlative neurophysiological studies of the external genitalia of the bull and the ram", *American Journal of Veterinary Research*, vol. 19, pp. 853-865.

Larson, L. L., Kitchell, R. L., & Campbell, B. 1961, "Neural mechanisms in sexual behaviour. III. Preputial muscles and their reflexes in bull calves and rams.", *American Journal of Veterinary Research*, vol. 22, pp. 37-42.

Long, S. E. 1969, "Eversion of the preputial epithelium in bulls at artificial insemination centres", *Veterinary Record*, vol. 84, p. 495.

Long, S. E. & Dubra, C. R. 1972, "Incidence and relative clinical significance of preputial eversion in bulls.", *Veterinary Record*, vol. 91, pp. 165-169.

Long, S. E. & Hignett, P. G. 1970, "Preputial eversion in the bull. A comparative study of prepuces from bulls which evert and those which do not.", *Veterinary Record*, vol. 86, pp. 161-164.

Breeding Soundness Abnormalities in Polled and Horned Bulls

- Lyne, A. G. & Hollis, D. E. 1973, "Development of horns in Merino sheep", *Australian Journal of Zoology*, vol. 21, no. 2, pp. 153-169.
- Madrid, N., Ott, R. S., Rao Veeramachaneni, D. N., Parrett, D. F., Vanderwert, W., & Willms, C. L. 1988, "Scrotal circumference, seminal characteristics, and testicular lesions of yearling Angus bulls.", *American Journal of Veterinary Research*, vol. 49, no. 4, pp. 579-585.
- Maleed, Z. Z. 1976, *Biometrical and functional studies on the penis in ruminants*, University of London, UK.
- McDiarmid, J. J. 1981, "'Corkscrew penis" and other breeding abnormalities in beef bulls.", *New Zealand Veterinary Journal*, vol. 29, no. 3, pp. 35-36.
- Mickelsen, W. D. & Memon, M. A. 2007, "Infertility and diseases of the reproductive organs of bucks," in *Current Therapy in Large Animal Theriogenology 2*, 2 edn, R. S. Youngquist & W. R. Threlfall, eds., Saunders Elsevier, St. Louis, Missouri, pp. 519-523.
- Milne, F. J. 1954, "Penile and preputial problems in the bull", *J.Am.Vet.Med.Assoc.*, vol. 124, pp. 6-11.
- Pailhoux, E., Vigier, B., & Chaffaux, S. 2001, "A 11.7-kb deletion triggers intersexuality and polledness in goats", *Nature Genetics*, vol. 29, pp. 453-458.
- Prayaga, K. C. 2005, *Genetic options to replace dehorning of beef cattle in Australia*, Meat and Livestock Australia. Final Report to Meat and Livestock AHW.094.
- Prayaga, K. C. 2007, "Genetic options to replace dehorning in beef cattle - a review", *Australian Journal of Agricultural Research*, vol. 58, pp. 1-8.
- Rice, L. E. 1987, "Reproductive problems of beef bulls.", *Agri Practice.*, vol. 8, pp. 22-27.
- Roberts, S. J. 1986, *Veterinary Obstetrics and Genital Diseases (Theriogenology)*, 3 edn, S.J.Roberts., Woodstock, Vermont.
- Santa Gertrudis Breed Society 2007, *Past, present and future of Santa Gertrudis* <http://santagertrudis.com/history.html>.
- Seidel, G. J. & Foote, R. H. 1969, "Motion picture analysis of ejaculation in the bull", *Journal of Reproduction and Fertility*, vol. 20, no. 2, pp. 313-317.
- Siebert, M. 1955 "Eine Studie iiber des Horn des Rindes und seine Genese mit eigenen Untersuchungen iiber den Bau und die Vererbung des Wackelhornes", Inaugural-Dissertation zur Erlangung des Grades eines Doktors der Veterinarmedizin an der Freien Universitat Berlin.
- Spitzer, J. C., Hopkins, F. M., Webster, H. W., Kirkpatrick, F. D., & Hill, H. S. 1988, "Breeding soundness examination of yearling beef bulls", *Journal of the American Veterinary Medical Association*, vol. 193, pp. 1075-1079.
- Steffen, D. 1997, "Genetic causes of bull infertility.", *Veterinary Clinics of North America.Food Animal Practice*, vol. 13, no. 2, pp. 243-253.

Breeding Soundness Abnormalities in Polled and Horned Bulls

Turner, L. B. An anatomical study of chronic preputial prolapse in Santa Gertrudis bulls. 2007a. Unpublished data

Turner, L. B. Reasons for culling bulls in Northern Australia. 2007b. Unpublished data

Vaiman, D. 2000, "Mammalian sex reversal and intersexuality: deciphering the sex determination cascade", *Trends in Genetics*, vol. 16, no. 11, pp. 488-494.

Van Camp, S. D. 1997, "Common causes of infertility in the bull.", *Veterinary Clinics of North America. Food Animal Practice*, vol. 13, no. 2, pp. 203-231.

Van den Berg, S. S. 1984, "An investigation into the etiology of prolapsing lamina interna in the Brahman and Santa Gertrudis breeds and the correction thereof.", *Proceedings 13th World Cong Dis Cattle*, vol. 2, pp. 745-746.

Venter, H. A. W. & Maree, C. 1978, "Factors affecting prolapse of the prepuce in bulls.", *J. South Afr. Vet. Assoc.*, vol. 49, no. 4, pp. 309-311.

Watson, J. W. 1966, *The artificial stimulation of ejaculation in the bull and angioarchitecture of the ruminant penis*, PhD, The University of Queensland, Australia.

Wolfe, D. F., Hudson, R. D., & Walker, D. F. 1983, "Common penile and preputial problems of bulls", *Compend. Contin. Educ. Pract. Vet.*, vol. 5, pp. 447-455.

12 Acknowledgements

The project team wishes to thank the following veterinarians and researchers for supplying their BBSE data and professional opinion:

Scott Parry – Coonamble Veterinary Clinic, Coonamble (NSW)

Ralph Kuhn – Coolah Veterinary Clinic, Coolah (NSW)

David Swan – Swans Veterinary Services, Esperance (WA)

Dr Eric Taylor – School of Veterinary and Biomedical Sciences, Murdoch University (WA)

Also the team wishes to acknowledge the statistical analysis provided by Mr Ricardo Soares from The University of Queensland's School of Veterinary Science.