FACTORS AFFECTING DEVELOPMENT OF HORNS AND SCURS IN DOMESTIC RUMINANTS

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SUMMARY

Most domesticated ruminants were naturally horned. Originally this was to help defend themselves from predators and compete for food resources and mating partners. Genetic control of the presence or absence (polledness) of horns or scurs (unattached horns) has been extensively investigated. However, variation in rate of development, size and shape of horns is also affected by non-genetic factors such as sex, nutrition, age and photoperiod. This study aimed to provide an overview of the impacts of these factors on horn development in different species of ruminants and to empirically investigate the interaction between genetics, sex and horn-status in 7 breeds of Australian beef cattle. This framework suggested that horns evolved through sexual selection, as horn ontogenesis is dependent upon genetics, sex of the individual and variation in testosterone.

INTRODUCTION

Cattle (*Bos taurus* and *Bos indicus*) and sheep (*Ovis aries*) are very important in livestock production systems world-wide because of the multitude of useful products derived from them and, their ability to be raised under highly variable environmental and management conditions. Both species typically grew symmetrical paired horns of various shapes and sizes, and these have become a prominent feature of the phenotypic diversity of modern breeds. Generally, the head-status in these species can be termed as *horned*: keratin coated permanent protrusions attached to the skull itself, *knob*: hard bony lump at horn site (sheep only), *scurred*: rudimentary horns loosely attached to the skin rather than the skull itself, and *polled*: complete absence of horns, scurs, and knobs (Duijvesteijn *et al.* 2018). Morphologically, horns are different than other horn-like structures, e.g., antlers. Horns are comprised of a bony core covered by a hard layer of keratinous tissue. The presence of *horns* and *scurs* is difficult to determine at an early age, because both originate postnatally as free-floating buds and subsequently, only the former fuses into the cranium (Dove 1935; Mariasegaram *et al.* 2010; Wiener *et al.* 2015). Generally, both species grow a pair of horns laterally on the head.

Horns are remarkably diverse in form and size, and were originally likely to help animals' defend themselves, and compete for food resources and mate partners (Kiltie 1985; Lundrigan 1996; Davis *et al.* 2011). However, given the complete absence of horns in females of some Bovids and comparatively smaller size of horns in females of others, it has been suggested that horns originated and evolved primarily as male weaponry (Marshall and Hammond 1914; Kiltie 1985). In various species, diversity in horn shape and size has been associated with different types of agonistic male-male behaviours – namely stabbing, wrestling, fencing and ramming (Geist 1966).

Further, it has been suggested that there may be a link between horn development, dominance and fertility in males (Lundrigan 1996). Thus, differences in horn development between males and females could have been modulated by selective pressure, with larger horns becoming important traits of sexual selection in males, whereas in females less direct selection for horns resulted in considerably lower diversity in horn phenotypes (Bro-Jorgensen 2007; Stankowich and Caro 2009; Davis *et al.* 2011).

Cattle and sheep have been extensively investigated for the role of genetics in horn phenotype. Although a clear understanding of the genes and biological pathways involved is yet to be achieved, gene mapping strategies have led to development of diagnostic tools for early-in-life prediction of horn phenotype (Connors *et al.* 2018; Duijvesteijn *et al.* 2018; Randhawa *et al.* 2019). Evidence suggests that genetics of the individual determines the horn status as a qualitative trait, however, sex of the individual partly controls horn morphology. Studies on nutritional impact on horn development are very limited but has been shown to be important in some species (Monteith *et al.* 2018). Generally postnatal growth of horns up to maturity is linked to body growth, although in some species the horn grows continuously or periodically throughout life (Rughetti and Festa-Bianchet 2011; Wiener *et al.* 2015). Photoperiod has been reported to regulate horn growth in Iberian ibex (*Capra pyrenaica*), Spanish ibex (*Capra pyrenaica hispanica*) and two European mouflon species (*Ovis orientalis musimon* and *Ovis gmelini musimon*). Also in these species variations in testicular function and plasma concentrations of testosterone and prolactin at different ages have been linked to rate of horn growth (Toledano-Diaz *et al.* 2007; Santiago-Moreno *et al.* 2012). Development of horns has shown diverse patterns in beef cattle. The objectives of this study were to review aforementioned factors influencing horn growth in bovids and to investigate the interaction between genetics and sex in Australian beef cattle.

MATERIALS AND METHODS

Phenotypic information about head-status (*horn*, *scur*, *poll*) and sex (male, steer and female) from 6,664 registered animals of 7 breeds in Australia (Table 1) were obtained from the BREEDPLAN database (http://breedplan.une.edu.au/index.php). Accuracy of assignment of head-status phenotypes can be compromised by several issues, including often failing to be able to differentiate between *horn* and *scur* prior to dehorning as a calf, late onset of *scurs*, incorrect assignment of cattle as *poll* when in fact they were dehorned and data transcription errors. To better understand the potential prevalence of these inaccuracies, a resource population of Droughtmaster cattle owned by The University of Queensland (UQ-herd) was phenotyped by two experienced beef cattle research scientists (Table 1). Genotypes on each animal of the UQ-herd (n=84) and samples previously collected (n=6,664) for BREEDPLAN were analysed using the 5-SNP markers in the POLL region applied through the optimized poll testing (OPT) assay (Randhawa *et al.* 2019).

Table 1. Number of samples tested, and cattle by sex and head-status phenotypes

Breeds	Number tested	Sex			Head-status		
		Male	Steer	Female	Horn	Scur	Poll
Brahman	2722	1772	191	759	2138	130	454
Charolais	517	351	-	166	63	9	445
Droughtmaster	488	114	278	96	102	114	272
Hereford	2740	1997	264	479	415	139	2186
Limousin	24	20	-	4	3	2	19
Santa Gertrudis	108	103	1	4	42	11	55
Shorthorn	65	51	-	14	-	-	65
Total	6,664	4,408	734	1,522	2,763	405	3,496
(%)	(100)	(66.2)	(11.0)	(22.8)	(41.5)	(6.0)	(52.5)
UQ-herd	84	9	-	75	15	23	44

RESULTS AND DISCUSSIONS

Table 2 shows the distribution (%) of head-status within each sex for various genotypes determined by OPT. Genotypes represent different combinations of the copies of *horn* (H) and *poll* (Pc & Pf)

alleles (Randhawa *et al.* 2019). Pc and Pf are denoted for Celtic and Friesian types, respectively, both sequence variants associated with polledness in cattle (Medugorac *et al.* 2012; Allais-Bonnet *et al.* 2013; Wiedemar *et al.* 2014). Theoretically, single gene-based inheritance suggests that HH animals grow *horns*, HP (HPc or HPf) grow *scurs* and PP (PcPc, PcPf or PfPf) are *polled*. In reality, translation of genotypes to phenotypes is complex for HP. Overall, phenotypic concordances of HH, HP and PP indicated considerable ambiguity in the BREEDPLAN data (Connors *et al.* 2018). HH and PP deviations (less than 5%) are not plausible to any known factor affecting horn development in male and female cattle. However, note that HH steers had the highest frequency of *scur* (8.12%) and *poll* (7.78%) phenotypes, because castration would have caused a cessation or delayed horn growth resulting in misclassification of phenotypes. Genotypes of the UQ-herd were 100% consistent for expected phenotype, except HPc (53%) and HPf (100%) in females were *polled,* when they were expected to be scurred. Interestingly, both data also showed that carriers of Friesian allele (HPf) are more likely to be *polled* than *scurred* as compared to Celtic (HPc) across all sex-classes. Pf has been speculated as more likely to be a causative variant (Wiedemar *et al.* 2014), whereas, gene-edited introgression of Pc has successfully produced *polled* calves (Carlson *et al.* 2016). Different gene pathways have been shown to be involved in horn and scur development (Mariasegaram *et al.* 2010). Previously, horn and scur growth control by two loci (genes), i.e., Poll (P/p) and Scur (Sc/sc), has been debated and the gene-pair interactions postulated that horns are developed by pp (HH) regardless of Sc/sc alleles, however, ScSc cause scurs for PP males and females as well as Pp males can scur with either ScSc or Scsc while Pp female can only scur when ScSc (Long and Gregory 1978). Our results contrast to this model because scurs in PP were rarely observed (5 out of 428), seemingly errors, in limited breeds (4 Droughtmaster and 1 Hereford), which is in line with the findings that only Pp can cause scurs (Wiedemar *et al.* 2014). On the other hand, sex hormones affecting horn agenesis in goats (Pailhoux *et al.* 2001) and morphological alterations in sheep (Marshall and Hammond 1914) suggest sex specific horn regulation , horn dysmorphism or complete agenesis. Our observations warrant further investigation about the perceived involvement of the Sc gene (Tetens *et al.* 2015), and the role of the peripubertal changes in sex-hormones affecting phenotypes for HP (Pp).

Table 2. Distribution of Poll gene tested genotypes for sex-wise phenotypes in cattle breeds

Genotypes	N	Male head-status (%)			Steer head-status (%)			Female head-status (%)		
		Horn	Scur	Poll	Horn	Scur	Poll	Horn	Scur	Poll
HH	2,623	95.6	3.06	1.28	84.1	8.12	7.78	96.2	1.59	2.17
HPc	2,057	15.4	17.8	66.6	10.2	19.1	70.6	8.48	5.05	86.5
HPf	120	2.60	7.80	89.6	-	-	100	3.33	3.33	93.3
PcPc	1,570	0.85	0.08	99.1	0.85	2.56	96.6	0.40	-	99.6
PcPf	267	0.45	0.45	99.1	-	-	100	-	-	100
PfPf	27	-	-	100	-	-	100	-	-	100
HP *	2,177	14.7	17.3	68.0	9.80	18.3	71.9	8.19	4.95	86.9
PP *	1,864	0.77	0.14	99.1	0.76	2.27	96.9	0.33	-	99.7
UQ Herd										
HH	15	100	-	-	-	-	-	100	-	-
HPc	43	-	100	-	-	-	-	-	47	53
HPf	2	-	-	-	-	-	-	-	-	100
PcPc	24	-	-	100	-	-	-	-	-	100

* Combined distributions of heterozygous HP (HPc+HPf) and homozygous PP (PcPc+PcPf+PfPf).

CONCLUSIONS

Form and function of headgear vary in each horned species. However, most ruminant species can be recognized by the unique shape and size of male horns, which are primarily used as anti-predators and to combat for mating partners. Given the evolved involvement of horns in sexual selection, horn growth is dependent upon genetics and sex of the individual. Not only the gender itself, but also variation in the sex related hormones (e.g., lower testosterone in steers) can impact the appearance and growth of horns and scurs. As such, the trait is complex and our empirical data suggested that visual detection of head-status is challenging leading to ambiguous classifications, and this error is minimised when phenotypes were assessed within the UQ-herd by skilled personnel. In future study, it is hoped that heterozygous animals expressing as *poll* and *scur* can be used to elucidate whether the scur phenotype is influenced by sex (hormones) or an entirely separate gene.

ACKNOWLEDGEMENTS

Meat and Livestock Australia provided financial support for this project (L.GEN.1713).

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