Breeding Focus 2021 - Improving Reproduction

Edited by

Susanne Hermesch

Animal Genetics and Breeding Unit, University of New England, Armidale, Australia

Sonja Dominik

CSIRO Agriculture and Food, Armidale, Australia

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Preface

“Breeding Focus 2021 – Improving reproduction” is the fourth workshop in the series. The Breeding Focus series was developed to provide an opportunity for exchange between industry and research across a number of agricultural industry sectors. With this goal in mind, workshops have included presentations across multiple agriculturally relevant animal species to take participants outside their area of expertise and encourage them to think outside the box. Reproduction is a main driver for profitability and genetic gain. We will discuss existing knowledge, identify gaps and explore genetic and management strategies to improve reproduction further in multiple species.

Successful reproduction is a complex characteristic comprising the formation of reproductive cells, successful mating and fertilisation, embryonic and fetal growth and eventually a successful birthing event. In livestock species, reproduction traits have mostly low heritabilities, which makes it challenging to improve reproduction as part of a multiple trait breeding objective. The complexity arises not just from the cascade of processes required to result in successful reproduction, but the relevant traits are different in males and females and they are influenced through health and fitness, nutrition, climate and other environmental and management factors.

Challenges to the improvement of reproduction can vary widely for different species. For less domesticated species such as abalone, the ability to produce and reproduce the animals in captivity presents a major challenge. In bees, reproduction has not been given great attention and little research has been undertaken to understand the underlying genetics of drone and queen reproduction. However, in all industries reproduction is recognised as the basis for genetic and economic gain. It directly influences the selection intensity that can be applied. It also determines how many animals are not required for replacement and can be sold. In all industries, irrespective of the challenge, cost-effective and easy to measure phenotypes of reasonable heritability are central. New technologies and approaches enable the development of novel phenotypes for genetic improvement which will be combined with a growing amount of genomic data in livestock species and together these developments provide new and exciting opportunities to improve reproduction further.

We would like to thank everyone who has contributed to this event for their time and effort: the authors for their contributions to the book and presentations, the reviewers who all readily agreed to critique the manuscripts. We would like to express a special thanks to Kathy Dobos for her contributions into the organisation of this workshop and the publication. Thank you!

Susanne Hermesch and Sonja Dominik

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Climatic constraints facing sheep reproduction

Gordon Refshauge[1] *and Simon de Graaf*[2]

[1]New South Wales Department of Primary Industries, Cowra, NSW 2794, Australia

[2]The University of Sydney, Faculty of Science, NSW 2006, Australia

Abstract

Increasing climatic variability can be expected to challenge the health, welfare and productivity of sheep, globally. Cold temperatures are broadly recognised to affect reproduction via an increase in neonatal lamb mortality from exposure to combinations of cold, wet and windy conditions, but such conditions are rarely implicated in the reduction of ewe or ram fertility. The opposite is generally true for heat stress; the impact of heat stress on reproduction is not widely recognised and its ability to impair reproduction is most likely to affect the fertility of ewes and rams. Heat stress, however, arguably poses a broader risk to sheep reproduction than cold exposure, because the components most at risk of impairment are so wide ranging. Gametogenesis, follicle development, ova quality, embryo survival, placental vascularisation leading to impaired fetal growth, lactation and lamb survival may all be negatively affected by heat stress. The sheep, with a 5-month gestation, invariably negotiates climatic extremes at key times of reproduction. Given there is limited evidence indicating mammals can be simultaneously tolerant of heat and cold stressors, somewhere in the middle is a compromise around the time of mating, which suggests the potential to select for thermal tolerance in either direction. In other species, selection for growth and muscling increases susceptibility to heat stress, and in the Australian sheep, a greater emphasis is being placed on these traits. It is not known if such recent selection increases vulnerability to heat stress. The question is, as the climate continues to rapidly warm, which thermal extreme do breeders select for, if indeed they have been, or will, or can?

Changing climate and animal welfare and productivity

Our rapidly changing climate is already presenting threats and opportunities for sheep producers in Australia and long-term adaptation will require a range of transformational changes (Rickards and Howden 2012). For example, the gradual southern shift of sub-tropical weather systems offers opportunities to expand the area suitable for sub-tropical pasture species. Highly productive perennial species such as Buffel, Panic and Digit grasses, as well as summer annual forages offer potentially enormous amounts of grass production per hectare, enabling the flexibility in the feedbase under future climate scenarios. Current research explores the suitability of these forage types and will provide options for producers in the future (Boschma *et al.* 2017; Boschma *et al.* 2021). New threats require careful thought, however, for diseases such as the southern reach of previously non-endemic gastro-intestinal worms, and more frequent summer storms and associated sheep blowfly burdens (Henry *et al.* 2012). Heat stress has been omnipresent in many sheep growing environments across Australia, but the frequency and intensity of heat waves are rising (Steffen *et al.* 2014), presenting a new threat too.

Climate change is anticipated to broaden temperature extremes, suggesting that cold stress events will be less frequent but not unlikely and have the potential for greater severity. The impact of cold stress on sheep production is greatest in the first fortnight after shearing for grown animals and around the time of birth in the neonate and are characterised by acute events brought about by a combination of temperature, rain or wind. The impacts on sheep are obvious because they are visual. The impact of mortality is economic and together with concerns for productivity and welfare has led to warning systems for graziers, such as the Sheep Graziers Warning. In contrast, there is no such public warning system for heat stress and livestock, although the Katestone website for dairy (https://dairy.katestone.com.au) and the Cattle Heat Load Toolbox for beef feedlots (https://chlt.com.au) offer opportunities for advanced preparations ahead of heat waves.

Heat stress is known to impact on the productive and reproductive potential of ruminant livestock (Sejian *et al.* 2019). Sheep are considered more tolerant to heat stress than cattle (Silanikove 2000), yet recent work by van Wettere *et al.* (2020) has estimated heat stress costs the Australian sheep industry around $97-168 M per annum. The assumptions behind the costs include the time of mating, the number of sheep located in heat stress susceptible regions and the size of the impact at different surface temperature scenarios (current, +1°C and +3°C). Under future climate scenarios that cost is expected to increase to $166-278 M. NSW DPI is undertaking climate vulnerability assessments for numerous agricultural and horticultural enterprises that will enable heat and cold stress impacts to be modelled for sheep reproduction using historical and climate change scenarios (www.dpi.nsw.gov.au/climate-and-emergencies/climate-change-research-strategy/vulnerability-assessment).

Much of our knowledge on the impact of heat stress on sheep reproduction is dated, with much work in the 1960s to 1980s, but little since, and most of that work undertaken using the Merino breed (Table 1A and 1B). Amongst that early work, some authors suggested heat waves lasting 7 days in duration were unlikely to occur under Australian conditions (Thwaites 1971), but were able to demonstrate short heat waves of 3 days duration impaired pregnancy outcomes. Furthermore, the models to determine the wind chill index were developed on sheep using 1960s breeding objectives and considerably lower reference bodyweights (Donnelly 1984) and, like the historical heat stress studies, require modernising.

This review aims to consider how climate places constraints on sheep reproduction. Of particular interest is the congruence of heat tolerance with cold tolerance and the traits that may be important to future breeding objectives and how these may be measured.

The effects of cold exposure on sheep reproduction

Cold stress does not appear to adversely affect the ability of sheep to conceive; for the ram at least, the scrotum appears to be a sufficient insulator, as briefly discussed by Moule and Waites (1963). Oestrous behaviour has been suppressed in crossbred ewes that were either fasted or freshly shorn before experiencing days of low minimum mean temperatures (0.6°C), rain, snow and strong winds, but was not depressed in *ad libitum*-fed and unshorn ewes (MacKenzie *et al.* 1975). In that study, follicular activity and ovulation rate were not affected. Griffiths *et al.* (1970) were able to successfully reduce ovulation rate in Scottish Blackface ewes, but required up to 42 days of exposure (17 days pre-breeding and 25 days post-breeding) to 6 hours daily of wetting (25-75 mm) in autumn, in Scotland. Embryo loss was also elevated in those ewes exposed to the chill conditions post-mating. The conclusion drawn is that cold stress poses a relatively minor risk on the ability of ewes to reproduce. However, successful reproduction requires high levels of lamb survival and this is when cold stress plays its most important role.

The current best practice management recommendations to improve sheep reproduction include various tangible, measurable targets for improvement and optimisation. These include bodyweight, body condition and nutrition targets pre-mating and throughout pregnancy, differential ewe management according to litter size and the preparation of lambing paddock feed on offer. Notwithstanding the benefits created by adherence to current best practice management targets, the impact of severely cold and wet weather coinciding with the peak lambing time can rapidly unwind the efforts of best management practice and lead to high rates of lamb mortality.

Lethal hypothermia is the loss of body heat, culminating with the death of the animal. For neonatal lambs, starvation and exposure are commonly grouped together, with the inseparable mismothering, as a complex set of interactions and effects that are associated with the mortality of many or most lambs (Luff 1980). At its worst, reported losses to cold exposure have been as high as 91% (Obst and Day 1968). Lambs that do not suckle will die and cold weather accelerates that timeframe (Haughey 1980). Furthermore, cold lambs also struggle to suckle milk (Dwyer 2008).

Other interacting factors affect the mortality in for newborn lambs. Subjectively assessed hypoxia-caused cranial and spinal lesions, as a consequence of difficult or slow birth, are associated with the mortality of up to 39% of lambs (Refshauge *et al.* 2016), and vascular lesions of the central nervous system have been associated with hypothermia (Alexander *et al.* 1980). These hypoxic neonatal lambs have impaired thermogenesis, teat seeking and suckling abilities (Eales *et al.* 1982; Dutra and Banchero 2011). Susceptibility to cold stress is increased following insult to the central nervous system, which is most likely a function of parturition duration (Dutra and Banchero 2011). However, exposure of ewes to cold weather 7 or 14 days pre-partum has been also associated with increased dystocia and starvation/mismothering (Everett-Hincks and Dodds 2008). Thus, cold stress alone may be detrimental to lamb survival, but other factors associated with the gestation and the birth process heighten the susceptibility to cold weather.

The impact these combined factors have on the neonate lead to elevated requirements for energy as heat loss exceeds endogenous heat production. Summit metabolism is the highest level of heat production obtainable at normal body temperature, without voluntary muscle activity (Alexander 1962). The factors affecting summit metabolism and vulnerability to cold exposure include litter size, birth weight, birth coat, skin thickness and breed.

The measure of coldness is the wind chill index, a calculation of ambient temperature, rainfall and wind speed. For most Australian environments and times of the year of lambing, high wind chill index days require all three components to be forcing. However, there are some locations and times of the year when temperature and wind is all that is required to meet high risk conditions (Broster *et al.* 2012).

Twin-born, lighter weight and Merino lambs are each more susceptible to wind chill than singles, heavier weight and crossbred lambs (Donnelly 1984). This work was undertaken in the early 1970s and there may be value in updating these relationships for the modern sheep breeds as selection for fat, muscle, growth and lamb survival have received increasing attention in the last decade. Furthermore, new breeds and types, such as the shedding, composite and modern Merino are heavier, higher performing animals with different breeding objectives than the 35-55 kg Merino or 45-65 kg crossbred of the late 1960s. An example of breed differences in thermogenesis is found between purebred and crossbred lambs (Plush *et al.* 2016b) and more work may be required to understand wind chill index relationships with newer breeds, to enhance the existing sheep grazier alert warning system.

Defining ambient heat stress conditions

Heat stress is defined as the demand made by the environment for heat dissipation (Silanikove 2000). Normal body temperatures for sheep range between 38.8 and 39.7°C (Roger 2008) and hyperthermic animals have body temperatures above the upper limit. This can result in body temperatures nearing 40°C, after which there are quite serious implications for normal cell function. For example, the review by Moule (1954) indicates an uncoordinated gait may be observed in sheep with body temperatures greater than 43.3°C. Sheep manage increasing heat load through sweating and panting, with rapid shallow breathing increasing in rate to include deeper breaths as heat stress increases (Hales and Webster 1967); although sweating is less effective due to the fleece (Marai *et al.* 2007). Rectal temperature remains normal until the stress load increases beyond the ability of breathing and sweating to manage homeothermy. Normal respiration rates are considered between 17 to 22 breaths per minute (Roger 2008) and thus both body temperature and respiration rate can be used to determine a sheep's thermal state by measuring these two response variables. However, because body temperature is under homeostatic control, respiration rate will indicate stress earlier than body temperature.

A chronological list of Australian studies examining the effects of heat stress is provided in Table 1A and 1B.

An index of human discomfort was proposed by Thom (1959), which was subsequently modified for cattle and has been reported for sheep by Srikandakumar *et al.* (2003), Al-Haidary *et al.* (2012) and most recently by van Wettere *et al.* (2020). The modified Thom index has thresholds proposed for dairy cattle, including alert, danger and emergency phases of heat stress, but no such levels are indicated for sheep. An alternative temperature humidity index (THI) was proposed by Marai *et al.* (2007) and the equation is as follows:

$$THI = db°C - ((0.31 - 0.31RH\%)(db°C - 14.4))$$

where db°C = dry-bulb temperature and RH = Relative Humidity.

While this index offered thresholds for sheep, these failed to make logical sense because extreme heat load conditions were relatively mild in temperature and humidity. For example, “extreme severe heat stress” was attained at a value exceeding 25.6, such as 29°C and 20% RH. Recent work has proposed alternative thresholds for this equation (Lees *et al.* 2017). These are: Extreme heat stress has a THI >32.3, High heat load is proposed as THI >28.6 to ≤32.3 and moderate heat load is THI >24.3 to ≤28.6. No heat load conditions are those THI ≤24.3. These categories are defined by significantly different rumen temperature and respiration rates. Where listed, all data presented with a THI throughout this chapter refers to the Marai index.

The effects of heat exposure on sheep reproduction

Heat stress in ruminants has four primary effects on flock reproduction: reductions in pregnancy rate, restrictions to fetal development, elevated lamb mortality, and reduced milk production and quality. The following discussion on heat stress and its impacts on sheep reproduction are presented under these four main groupings.

Table 1A. Studies from 1956 – 1975. Breeds, experimental treatment and duration and outcomes for Australian-based studies examining heat stressed reproduction. Where reported, temperature humidity index (THI) is the equation reported by Marai et al. (2007)

Author	Breed	Treatment	Outcomes
Yeates (1956)	Merino	Climate chamber. Ewes exposed to 41°C for 7 hours per day, 110-148 days or 44 °C for 7 hours per day, 110-148 days.	Lower fertility.
Moule and Waites (1963)	Merino	Climate chamber. 40.5°C, 8.5 mm Hg vapour pressure and 40.5°C, 31.5 mm Hg. Two 6 h bouts, two days apart.	One-quarter of rams severely affected, sperm concentration decreased in all rams 13-52 days after treatment.
Shelton (1964)	Rambouillet	Climate chamber. Ewes exposed to 37.8°C to 40.6°C, 10 hr daily, lasting from the end of mating to lambing.	Lower birth weight and lower survival (78.9% v 36.4%).
Alexander and Williams (1966)	Merino	Climate chamber. Ewes exposed to 44°C for 9 h, 33 mm Hg, and to normal temperatures for 15 hours, Day 40 to 96 gestation or from Day 40 to 144. Night temperatures were ambient and autumn or winter.	Little impact on fetal growth.
Thwaites (1967)	Merino, Southdown	Climate chamber. Ewes exposed to 37.8°C or 35°C at 55-60 RH% for 20 days post-conception. THI >34.5 or >32.1.	High return to oestrous and high embryo mortality.
Thwaites (1969)	Merino	Climate chamber. Ewes exposed to 41.1°C at 40 RH% (THI 36.1) with night conditions 35°C and 30 RH% (THI 30.5) for 15 days post-conception. Ewes constantly held in heat stress conditions. Shorn v unshorn comparison.	100% embryo loss in heated and unshorn ewes, 66.6% in unshorn heated ewes. Each were higher than control ewes.
(Thwaites 1971)	Merino	Climate chamber. Ewes exposed to 40.6°C and 30 RH% (THI 34.9) applied for 3 or 6-day periods at different times after mating.	Elevated embryo loss in ewes heated for Days 1-4 (54.5%) and Days 1-7 (83.3%) post-mating.
Lindsay *et al.* (1975)	Merino	Field study. Spring, summer and autumn mating. Naturally mated flocks. Temperatures ≥32.2°C or >35°C.	Lower pregnancy rate (r = -0.35) & fewer lambs born (r = -0.35).

Table 1B. Studies from 1979 – 1993. Breeds, experimental treatment and duration and outcomes for Australian-based studies examining heat stressed reproduction. Where reported, temperature humidity index (THI) is the equation reported by Marai et al. (2007)

Author	Breed	Treatment	Outcomes
Sawyer (1979)	Merino	Climate chamber. Ewes exposed to 40-43°C for days 1-3, 1-6 or 1-9 post-conception.	Lower fertility.
Kleemann and Walker (2005)	Merino	Field study. Naturally mated flocks. Temperatures ≥32.0°C.	Lower fertility.
Hopkins *et al.* (1980)	Merino	Field study. Ewe rectal temperature recorded during 10 days of January when temperatures were observed between 37 to 43°C, and during the last 4 months of gestation, temperatures were observed between 33 to 41°C.	Lower birth weight (1.4 to 1.6 kg/°C) and greasy fleece weight
Hopkins *et al.* (1980)	Merino	Climate chamber. Ewes maintained body temperature about 40°C for at least 16 hours each day, from Day 117 of gestation to lambing.	No impact on feed intake. 33% lower birth weight, 9-13% smaller body dimensions.
(Davies *et al.* 1984)	Crossbred	Climate chamber. Ewes exposed to 43°C for 8 hours each day for 5-7 days, from Day 113 to 142 of gestation.	Higher ewe cortisol and fetal lactate.
McCrabb *et al.* (1992)	Merino	Climate chamber. Ewes exposed to 42°C for 9 hours and at 32°C for 15 hours, Days 30 to 80 of gestation. Remaining ewes remained housed at comfort until D140.	Lower placental weight at D80 and D140. Lower fetal weight at D140, not D80.
(McCrabb *et al.* 1993)	Merino	Field study. Ewes selected for high (≥39.9°C) or low (≤39.8°C) rectal temperature. November mated.	Lower pregnancy rate (50% v 77%). Lower birth weight and Ponderal Index.

Reduction in pregnancy rate

Mediated by effects on rams

Semen damage is directly related to elevated subcutaneous scrotal temperature (Marai *et al.* 2007) and maintaining about 4°C difference between testicular and body temperature is important for spermatogenesis. The effects on sperm quality are generally delayed; Howarth (1969) showed no effects on semen quality during experimentation (4 days at constant 32°C, 65% RH; THI 30) but 1 week later motility and sperm concentration declined and the proportion of abnormal sperm increased and the negative effects worsened for 3 further weeks. The most heat sensitive rams have damaged spermatozoa evident from 13-14 days after heat stress and continuing throughout the study period, while in less severely affected rams damaged spermatozoa were evident later, from 14-20 days and sperm concentration decreased in these rams 21-32 days later (Moule and Waites 1963). Semen characteristics in the less severely affected rams were impaired to a lesser degree throughout the study and those characteristics recovered faster than the most stressed rams. Using wrinkly versus plain bodied rams, Fowler and Dun (1966) demonstrated that after a 3 day heat stress challenge (35°C, 50% RH; THI 32.1), sperm remained viable in all rams for 12-18 days, thereafter rapidly declining. Plain bodied rams showed no negative effects, while high wrinkle rams took 7-28 days to return to normal sperm concentration, while sperm motility and the percentage of live sperm took 30 to 55 days to recover. A temperature (*in vitro*) of 38.5°C is sufficiently hot to damage spermatozoa (Rahman *et al.* 2014) and the effects are severe at 41°C. Moule and Waites (1963) concluded that it was the ability of the scrotum to manage subcutaneous temperature that affected spermatogenesis. In that study, rectal and flank temperatures were not related to the effects on semen quality, indicating that the measure of temperature in rams focus on devices designed to measure scrotal temperature during heat waves. The major consequences of impaired spermatogenesis apply to flock reproduction rates via poor ova fertilisation and reduced embryo survival (Ulberg and Burfening 1967).

Mediated by effects on ewes

Fertility has been shown to decrease in naturally mated flocks when maximum temperatures are ≥32°C (Lindsay *et al.* 1975; Kleemann and Walker 2005). Climate controlled facilities and controlled breeding techniques have been able to be more specifically identify when heat stress has its greatest impacts on mating success.

Dutt (1963) reported that ewes in a heat stress treatment group during autumn while held at 32.2°C on the day of mating did not conceive. Ewes treated to that temperature 1, 3 and 5 days after breeding had better ewe fertility rates, but still substantial losses were incurred. The lowest ova fertilisation (40.7%) and highest per cent abnormal ova (55.6%) occurred when ewes were exposed to heat in the 5 days before breeding, when compared to the day of breeding (69.2% and 46.2%, respectively) or 1 day after breeding (100% and 30.8%, respectively)

(Dutt 1964). Sawyer (1979) reported similarly that the number of ewes which conceived and eventually lambed was reduced by exposure to high environmental temperatures shortly after insemination. The most critical period appears to be 5 days before and the first 3 days after insemination, outside this period fertility is only marginally reduced, if at all.

Hopkins *et al.* (1980) observed that spring joined ewes that failed to rear any lambs had rectal temperatures that were 0.3°C higher during a January heat wave (ambient conditions ranging from 37°C to 43°C) than ewes that reared lambs (40.1°C v 39.8°C). Dutt (1964) observed elevations of maternal rectal temperature up to 1.7°C were associated with the exposure to heat, and that the ewe temperature remained elevated up to 24 h after the exposure. In naturally mated flocks chronic heat stress is required to detect its impacts, but in artificially inseminated flocks, the timing of heat exposure becomes critical. Using 4 years of records in nearly 9,000 inseminated ewes, Santolaria *et al.* (2013) showed a 6% lower pregnancy rate when ewes held at pasture were exposed to daily maximum ambient temperatures >30°C within 2 days before insemination.

General impairment of hormone activity and oxidative stress in ewes and rams

In rams and ewes, heat stress can impair hormone function directly, or via reductions in feed intake, or via increased cortisol production. Each pathway lowers gonadotrophin-releasing hormone (GnRH), the reproduction governing hormone (Aggarwal and Upadhyay 2011).

In the female, heat stress also disrupts the normal release of luteinising hormone (LH) secretion, follicle-stimulating hormone, oestradiol, inhibin, androstenedione, prostaglandin and progesterone. However, the observations of these effects vary greatly between studies and species. A common conclusion is that heat stress changes the concentration of these hormones and is generally detrimentally, see reviews by Aggarwal and Upadhyay (2011) and Hansen (2009). Under chronic heat stress conditions, blood flow to the ovaries can decrease in preference to the skin, further lowering nutrient transfer, follicle dynamics and oocyte quality (Aggarwal and Upadhyay 2011). Taken together, hormonal disruption affects sexual activity, the duration of oestrous, the quality of the follicles and ova, lowering embryo quality and increasing the likelihood of less successful reproduction. In the ram the impact on GnRH and LH affect sexual activity and spermatogenesis via damage to spermatocytes and spermatids, resulting in lower semen volume, sperm motility, and increased percentages of abnormal spermatozoa. Good examples of the effects of heat stress on sperm quality attributes can be found in Moule and Waites (1963) and Fowler and Dun (1966).

Disruption of hormone release is not the only pathway to lower pregnancy rates. Damage to sensitive germ cells and gametes readily occurs in the presence of oxygen radicals. In the pre-ovulatory period, the follicle and oocyte are susceptible to elevated body temperatures (Roth 2008) and damage from metabolites called reactive oxygen species (oxygen radicals such as superoxides, peroxide and hydroxyls), which are stimulated in production by heat stress

(Hansen 2009), but susceptibility to which declines as oocyte development proceeds. Reactive oxygen species activity increases in oviducts and embryos (Matsuzuka *et al.* 2005). The effects of oxidative stress in the male also include compromised DNA integrity in spermatozoa (Pérez-Crespo *et al.* 2008), which are deleterious to fertilisation and development of resultant embryos.

Restrictions to fetal development

Chronic heat stress in the sheep is used as a model for intrauterine growth restriction. Long-term heat stress studies examining the effects on the fetus have exposed ewes to heat stress from Day 45 to Day 120 of gestation (Bell *et al.* 1987), or Day 65 to Day 141 (Bell *et al.* 1989). The impairment to birth weight represents fetal adaptation to a decreased placental ability to supply oxygen and nutrients. In both studies by Bell *et al.* (1987, 1989) placental and fetal weight was reduced, but only in the latter study was feed intake reduced. Andrianakis and Walker (1994) demonstrated reduced uterine blood flow, but not umbilical blood flow, and observed that individual animals had different responses within treatment, implying a degree of heat tolerance. Retardation of vascular endothelial growth factor expression in early pregnancy may also be a source of intrauterine growth restriction (Marai *et al.* 2008), suppressing placental vascular development. Davies *et al.* (1984) catheterised crossbred ewes and their fetuses in the third trimester and exposed the ewe to 43°C for 8 h over 5 days, resulting in increased fetal lactate, ewe cortisol and increased fetal breathing movements for up to 6 hours during the post-heat exposure recovery.

McCrabb *et al.* (1992) demonstrated negative correlations between placental and fetal weights with the rectal temperature of the ewe. When imposing heat stress at 44°C, Yeates (1956) were able to show reductions in birth weight. Alexander and Williams (1966) supported that finding, but only when night temperatures were also high in late gestation, whereby a substantial reduction in birth weight (0.9 kg) can occur. Wallace *et al.* (2005) showed that 40°C for 12 h, or 35°C for 12 at 30-40% RH (THI 30.8), from day 40 in gestation, with the treatment applied for variable time periods, will reduce birth weight. Reductions between 50-60% in birth weight were observed. The effects of chronic heat load continue to affect fetuses when the exposure continues for longer periods of time (80 days compared to 55 days) (Galan *et al.* 1999), thus the impact on the neonate can be lessened if the heat load can be removed earlier. High temperatures (37.8°C to 40.6°C) during gestation significantly reduced birth weight and increased lamb mortality (36.4% vs 78.9% lamb mortality) when compared to ewes held at cooler temperatures (23.9°C to 26.7°C) (Shelton 1964).

Decreases in birthweight are not mitigated by improved nutrition following impairment to blood flow. Diets offering a low plane of nutrition for the second half of pregnancy do not impair fetal growth when compared to ewes normally fed and heat stressed during the final third of pregnancy (Hopkins *et al.* 1980). The central nervous system appears to be vulnerable to maternal hyperthermia, with developmental and birth defects also possible (Edwards *et al.* 2003).

The effects on the neonate can be long lasting, with evidence for morphometric differences in bone lengths, reduced greasy fleece weight, possibly lower secondary to primary follicle ratio that results in lower fleece weights of higher fibre diameter (Hopkins *et al.* 1980). Greasy fleece weight (GFW) is lowered in progeny in direct relationship to ewe rectal temperature during mid-pregnancy, but the effect varies between years. Hopkins *et al.* (1980) reported that 58% of the variance in GFW from 26 month-old wethers was explained by maternal rectal temperature when recorded during a heat wave in late gestation, and 76% of the GFW variance in fleeces from 14 month old ewes. When the maternal rectal temperature record, taken in year 1 of the study, was included in the analysis for a second drop of lambs, the GFW in the 14 month-old ewe was affected, with 33% of the variance explained.

Elevated lamb mortality and reduced milk production and quality

Notwithstanding the clear impact heat stress has on fetal growth restriction, and the elevated risk low birthweight has for lamb mortality, heat stress poses additional risks to this relationship. Using spring-joined ewes, Hopkins *et al.* (1980), which was a field study undertaken at Julia Creek in northern QLD, also recorded rectal temperature in neonatal lambs and attempted to measure respiration rate. Breath rates were too high to accurately count, but rectal temperatures exceeded 40°C in all assessed lambs in the first 4 days of life. The breath rates remained extremely high during the day and only decreased in the late afternoon, after which the lambs fell asleep. This clearly increases vulnerability to starvation/mismothering and predators, the latter as suggested by Moule (1954). Mortality can be particularly high in hot environments, with Stephenson *et al.* (1984) reporting losses between 48-54% in unshaded lambing paddocks. Haughey (1980) recorded higher mortality in starved lambs at 40°C when compared to 28°C, but the highest mortality in that experiment occurred at 1°C.

Feed intake can also be impaired in heat stressed animals (Alexander and Williams 1966; Baumgard and Rhoads 2012), even though some studies do not show this despite other physiological responses, such as the animal house study undertaken by Hopkins *et al.* (1980). Reductions in feed intake may also affect milk yield (Baumgard and Rhoads 2012), but heat stress additionally lowers milk yield. Stage of lactation is a variable that affects response to heat stress (Fuquay 1981) and animals with higher milk yield are more susceptible to heat stress (Finocchiaro *et al.* 2005).

Genetic relationships of reproduction with thermal tolerance

Progeny testing for thermogenesis and cold tolerance was proposed by John Slee *et al.* (1991) as a means to breed more tolerant lambs, but to do so in a controlled and repeatable manner is not realistic (Plush *et al.* 2016a). Measures of skin temperature may provide a useful measure (McCoard *et al.* 2014) and their work points to breed differences in cold tolerance. Heritability estimates for cold resistance in Merino sheep are moderate and reported to be up to 0.7 ± 0.25 (Slee *et al.* 1991). That work also reported significant heritability estimates for birth coat (0.61 ± 0.24), coat depth (0.62 ± 0.24), skin thickness (0.35 ± 0.19), initial rectal temperature (0.38

± 0.20) and with genetic correlations between cold resistance and birth coat (0.56 ± 0.24), coat depth (0.56 ± 0.24) and skin thickness (0.51 ± 0.27). The opportunity for a favourable response to selection may be available, but it is not known how these traits correlate with other production traits. Rectal temperature was recorded in neonatal lambs, within 18 h of birth, in the Sheep CRC's Information Nucleus Flock, with a heritability of 0.10 ± 0.02 and favourable genetic and phenotypic correlations with lamb survival to weaning (Brien *et al.* 2010). To date, there appears to be just one gene marker (ADRB3) proposed for thermogenesis (Forrest *et al.* 2006).

Nardone *et al.* (2006) implies that the upper limit of the thermal comfort zone for highly selected animals is contracting and sensitivity to heat stress is rising. Genes associated with animal production, such a growth hormone, can be downregulated by heat stress. The review by Sejian *et al.* (2019) provides this example and also discusses other genes associated with animal production, such BMP, IGF-1 and leptin. Selection in favour of high-producing animals leads to increased metabolic heat production and concomitant susceptibility to heat stress, apparently irrespective of the species (Renaudeau *et al.* 2012). Those authors suggest considerable genetic variation for heat tolerance exists within and between species and breeds, but in tropical species the typical characteristics of heat tolerance includes small size, low productivity and specialised morphology, such as hair and sweating attributes (Renaudeau *et al.* 2012).

Heat tolerance in sub-tropical sheep, such as the Barbados Blackbelly varies between individuals (Ross *et al.* 1985). Temperature and respiration rates differed greatly between the breeds in that study, with the rectal temperature of the Dorset sheep being 0.5°C higher than the Blackbelly and Blackbelly x Dorset cross and respiration rate about 30 breaths per minute higher. British breed sheep may be more susceptible than Merinos (Yeates 1953), although little comparative research has been undertaken in Australia between breeds and crosses and in measuring components of reproduction (Table 1A and 1B).

Few genetic studies examining genetic variation for heat tolerance are available for Australian sheep and none have reproduction performance records. Rose and Pepper (2001) captured heritability estimates in Merino rams for rectal temperature (0.06 to 0.62) and respiration rate (0.13 to 0.67). In the corresponding paper on ewes, Rose and Pepper (2005) reported more moderate heritability estimates for rectal temperature (-0.01 to 0.34) and respiration rate (0.10 to 0.46). These studies show variation exists according to age, with higher heritability estimates observed for weaners than were observed for hoggets. Using cattle, Turner (1982) reported that rectal temperature had a heritability of 0.25 (± 0.12) and its genetic correlation with fertility was -0.76 (± 0.35), which may be a useful indication of what may be revealed if future research studies capture reproduction performance records in studies of thermal tolerance. Having selected ewes for high or low body temperature, McCrabb *et al.* (1995) found reasonable repeatability (r = 0.79 – 0.82) of rectal temperature across three years of the study, when recorded at 4 PM and under conditions of heat stress (THI 31.4 – 33.4).

Perhaps the most interesting genetic relationships between heat exposure and reproduction is that observed for heat tolerance and hypoxia. It is proposed that hypoxia may be a significant cause of death in neonatal lambs (Refshauge *et al.* 2016; Jacobson *et al.* 2020). In rats, various heat shock proteins confer differential tolerance to heat stress and hypoxia at the cellular level in *in vitro* studies (Heads *et al.* 1995), offering potential pathways for selection for improved heat tolerance and lamb survival. At the time of publication Sonna *et al.* (2002) listed over 100 different genes, including 55 heat shock proteins (HSPs) that were known to change their expression during or mostly, in response to heat stress. Sonna *et al.* (2002) listed the RNA binding protein CIRP gene as one that increases its expression after exposure to cold shock and hypoxia. Teague *et al.* (2017) has shown that *Drosophila* fruit flies have a positive genetic correlation ($r^2 = 0.3$) between flight under conditions of heat stress (39°C) and flight under conditions of hypoxia (12% O_2), but the respective correlation under normoxia conditions (21% O_2) was not present ($r^2 = 0.04$). The authors suggest that because insects rely heavily on aerobic metabolism during flight, it is possible the mechanisms share a similar or same genetic basis. Phenotypic features of insects adapted to low oxygen conditions include larger wings and smaller bodies, more efficient muscle fibres and higher mitochondrial densities or specialised metabolism. Also in fruit fly, mechanisms improving cellular sodium and potassium ion homeostasis appear to contribute to cold tolerance (MacMillan *et al.* 2015).

In general terms, the impact of cold stress is to slow enzymatic activity, whereas heat stress is an accelerator, but the physiological effects on cellular processes and proteins can be similar. As it is with heat stress, it is the duration of the cold stress event that has the most severe impacts on the cell (Sonna *et al.* 2002). Sonna *et al.* (2002) listed 17 genes whose expression changes during or mostly in response to cold stress. Of these, 6 are HSPs and 4 others are also genes changing expression after exposure to both heat and cold stress, such as cell cycle genes (p53, WAF1/p21), cytokines (IL8) and a heavy metal binding gene, metallothionein. Using kid goats, Jagan Mohanarao *et al.* (2014) identified HSP27 increased its expression in both cold and hot treatments.

Candidate genes were identified in a study of 32 cattle breeds (Freitas *et al.* 2021), using 982 animals. Many identified genes appeared to be pleiotropic, variously conferring adaptive advantage across heat and cold tolerance, immune response, oxygen transport, minimisation of oxidative stress, metabolic activity, feed intake, carcass conformation, fertility, and reproduction. Like many production traits thermal tolerance is a complex trait with many components which are difficult to measure. This may be a major challenge facing genetic adaptation to our rapidly changing climate. The breeds adapted to hot environments appeared to be more related to each other, while cold adapted breeds were equally related to each other, with the study by Freitas *et al.* (2021) identifying numerous genes potentially under selection for thermal tolerance.

Since the future climate is unknown, a selection strategy should retain a high level of adaptability to temperature shifts. Hence, the identification of genes conferring cold tolerance is required concurrently with identification and selection for heat tolerant genetic lines. The adaptive capacity of animals is reflected through various characteristics including morphological, anatomical, behavioural, physiological, biochemical, cellular and molecular. The value of anatomical adaptation may be questionable for sheep if that pathway increases susceptibility to heat loss during cold stress events, as we see with the goat and the susceptibility of the kid to cold exposure.

Goats are widely adapted, particularly to harsh environments and have developed mechanisms that permit survival at extremely hot and extremely cold temperatures (Jagan Mohanarao *et al.* 2014), but despite this, evidence is available to show that productivity still declines due to thermal stress (Al-Tamimi 2007). For example, 62% of Australian rangeland and crossbred kid mortality occurred when the wind chill index was greater than 950 kJ/m^2.h (Bajhau and Kennedy 1990), indicating a heightened sensitivity to cold stress. In the Merino lamb an equivalent level of mortality may be closer to 1100 kJ/m^2.h (Donnelly 1984).

The role of genomic selection (single nucleotide polymorphism (SNP) and/or functional genomics) remains uncertain. Reference populations need to be large for SNP-based genomics and likely requires locating in a hot environment. Functional genomics may require the collection of the most informative cell types (Sonna *et al.* 2002; Renaudeau *et al.* 2012). Furthermore, the cost of the genomic approach will need to compare favourably to the cost of collecting relevant phenotypes. However, next generation sequencing (NGS) technologies are suggested to enhance our understanding of complex thermotolerance mechanisms and pathways (Sejian *et al.* 2019). Hansen (2014) the potential for precision genome editing to create heat tolerant cells in susceptible breeds, and also discussed briefly seven genes with heat stress associated SNPs. Sejian *et al.* (2018) recommends effort must be directed to epigenetic changes to understand the differences in adaptive changes that are evolved over generation, which may help to understand the hidden intricacies of molecular and cellular mechanisms of livestock adaptation.

Few genetic selection flocks in Australia are currently suitable for selection to thermotolerance. The Merino Lifetime Productivity flock is most likely to meet the criteria of genetic diversity, scale, linkage and location; quite specifically the NSW DPI Macquarie site at Trangie, NSW, for heat stress and the CSIRO Armidale, NSW, site for cold stress. The MLA Resource Flock may be useful for the meat-focussed breeds too, with sites at Armidale NSW, Katanning WA and Temora NSW.

The pathway to trait selection for thermal tolerance to improve reproduction

Efficient data capture for selection for thermotolerance is the greatest challenge to further research and development because it requires experimental scale, genetic diversity, a wide range of samples and hot and cold stress events. Climate-controlled facilities are more suited to experimentation than for the exploration of genetic parameters. In most sheep production environments in Australia, thermal stress occurs as acute events, in short spells. During such events the livestock can modify their behaviour by seeking more shade, drinking more water and possibly altering feed intake. This will be scarce and difficult data to collect in the field. During chronic heat waves, more measurement opportunities will abound. Without engaging climate-controlled facilities, field observations will be relied upon. Scale can be obtained via field studies, but the ability to capture mass data cost-effectively remains a limitation. For example, to understand the impact of summer mating on sheep reproduction requires data capture at the point of pregnancy scanning to be collated with date of mating, location of mating, age and breed of the sheep and local factors that may explain random variation. Such data collection is technically feasible. The sheep and beef cattle sectors are at a considerable disadvantage when compared to pig and dairy industries with more intensive and regular performance measures.

Selection of animals capable of rearing lambs in hot environments should continue and the sheep industry should breed suitably adapted sheep or to otherwise provide shade (Hopkins *et al.* 1980). In contrast, recent climate modelling suggests genetic selection may not be necessary as a means for climate adaptation before the year 2070 (Moore and Ghahramani 2014).

Regulation of core body temperatures is a priority over several other physiological functions and the redistribution of blood flow (homeokinetic change) to regulate body temperature can compromise reproduction (Hansen 2009). Another homeokinetic change is the reduction of feed intake to lower metabolic heat production, when prolonged, reduced feed intake will have its own effects on reproduction outcomes. Adaptation (acclimatisation) includes a decline in anabolic and increase in catabolic hormones, such as higher prolactin to support homeothermy and lower thyroid hormone levels to reduce heat production (cited in) (Al-Haidary *et al.* 2012). In cold stressed animals, the physiological markers include decreased respiration rate and leptin, increases in metabolic rate (VCO_2), glucose, cortisol, T_3 (Plush *et al.* 2016b) the latter being stimulated by increased nor-epinephrine via the conversion of T_4 to T_3.

Measuring thermal tolerance

Understanding what to measure, how to measure it and how often is critical to the capture of data that will be valuable for genetic progress. Simplicity and accuracy are important considerations.

Panting score may be the most useful measure of heat stress in assessing animal welfare (Caulfield *et al.* 2014). The appeal of panting scores is two-fold. First, panting rises in response to small rises in body temperature. Second, the assessment is non-invasive, requiring minimal handling and can be collected *in situ*. The difficulty with pant score is recording individual information on large cohorts of livestock under heat stress conditions, and the cost of labour. Technological solutions are required for the capture of individual information to enable genetic parameter estimation. It is possible that ear tag sensors may be able to collect such information for sheep, as have recently been validated for use in cattle (Islam *et al.* 2020). The tags tested in that study were capable of detecting differences in the respiration rate of animals with different coat colours and between breeds and individuals.

The measurement of body temperature is the gold standard for heat stress. As an animal moves through states of higher stress, thermoregulation of the animals' set-point temperature will begin to fail and body temperature will rise to a new state. Technologies capable of serial recording of temperature have been reviewed by Lewis Baida *et al.* (2021) and offer much improved understanding of the effects of diurnal variation, accumulating heat load and experimental treatment effects. The types of devices vary from vaginal and rectal probes, rumen bolus, ear canal sensors, implantable or wearable devices. Thermal imaging using infrared thermography is also available for skin temperature measurement (Lees *et al.* 2018), so too are wearable global positioning (GPS) or navigation satellite systems (GNSS) enabling the study of behavioural acclimation (Lewis Baida *et al.* 2021).

Together panting score and temperature devices offer the ability to capture information on the individual which may lead to improved welfare outcomes. The true value of these devices, however, is how they will contribute to genetic datasets.

Adoption cycles

In addition to the predicted impacts of climate change and its wider impact on animal production and reproduction, of concern for industry must also be the slow rates of adoption of technology and strategies to improve reproduction. In a study that explored sheep producers attitudes towards the adoption of pregnancy scanning as a means to improve lamb survival, Elliott (2012) identified two groups of adopters: those driven to adopt by their attitude and those driven by emotions. At the time, little research had been done into the role emotions have in decision making, but that group was 52% of the sample. More recent work among Queensland cattle producers identifies the role of women in ag-tech adoption as essential to the decision-making process, particularly as the role of technology increases in agriculture (Hay and Pearce 2014) and this may well apply to the adoption of strategies to minimise the risk of climate extremes on future sheep reproduction. In a study of Italian researchers, extension specialists and sheep producers, different levels of knowledge on causes and consequences of climate change and different levels of trust in the mainstream narrative regarding climate change were sources for diverging attitudes towards climate change and the need for adaptation (Concu *et al.* 2020). Their results show that sheep farmers were less supportive of climate change adaptation, influenced by their knowledge of climate change causes and impacts and belief in climate science. While in Australia, livestock producers do recognise the relationship between animal well-being and productivity, and apparently place much emphasis on doing what they can to best manage adverse weather events (Buddle *et al.* 2021). Understanding producer attitudes to climate change will be critical to the success of any adaptation strategies. The report by Sudmeyer *et al.* (2016) highlights that some Western Australian farmers prefer information framed around business and profitability and all farmers preferred regionalised information that is locally relevant.

Conclusions and research gaps

The impact of cold stress on lamb survival is well established but appears not to affect mating success, although the sheep is a seasonal breeder with little successful mating occurring in the depths of winter. The range of consequences heat stress has for components of sheep reproduction are also well described. The timing and duration of heat waves in relation to the time of breeding will be key determinants affecting the outcome. There is some redundancy built into natural joining as this tends to be of 5-6 week duration in order to give ewes 3 periods of oestrus in which to get pregnant. As such, a heat event in one cycle should not dramatically impact the overall joining, so long as sperm quality of the rams has not been affected, as the ewes will simply cycle again and eggs fertilised in the ensuing cycle. However, this is not the case in artificial insemination programs where an acute heat waves has the potential to have a major effect given all ewes are programmed to conceive on the one day.

The correlation between ambient temperatures exceeding 32°C and reduced pregnancy rates is concerning and probably fails to resonate with Australian sheep breeders because 32°C is not very hot. Much of our understanding of the impacts of heat stress on reproduction stem from climate-controlled facilities that historically employed constant heating regimes or undertook their studies in cooler months to minimise the risk of acclimation on the findings. More recent studies employ diurnal heating regimes but none to date have studied reproduction. Overall, it is hard to translate known effects to the natural environment because so few reproduction studies explored sheep under natural conditions and incorporated measures of thermoregulation.

The rate of climate change and the expansion of the climate extremes might greatly challenge ruminant production systems. The ability of breeders to keep pace with the rate of climatic change will require a greater understanding of the adaptive mechanisms, physiological and biochemical pathways and consequences of current selection practices.

Breeds other than the Merino have rarely been utilised in reproduction studies related to thermal stress, particularly in Australian work. Breeds such as the Dorper, other shedding composites, woolled composite and woolled maternal breeds (e.g. Border Leicester x Merino) must have their thermal tolerance thoroughly examined. Of particular interest will be the plethora of genes available to support thermal tolerance that may well exist within and between these breeds. What are absent in the literature are genetic parameter estimates between thermal tolerance traits and the main production traits. This information will guide breeding and selection decisions and may instruct the industry about the seriousness of heat stress on future productivity. The technology appears to be ready for the measurement of body temperature and the necessary genetics resource flocks are currently available. Expansive sampling and genomic analyses will be required to identify as much diversity as possible. What also appears to be absent from the literature are good examples for lifetime or epigenetic effects.

Currently we may rightly presume that breeding sheep for thermal tolerance is indirect at best and is unlikely to be focussed and targeted at unfavourable weather events. It is not clear what attitudes Australian sheep breeders hold for the impact of heat stress on sheep reproduction, nor the impact that may have on adoption of any proposed genetic solutions. Given so little is understood about the genetic relationships between thermal tolerance and the key production and reproduction traits, there is much research, development and adoption required for the development of selection strategies.

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