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Effects of heat stress on the health, production and welfare of sheep managed on pasture

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Author: Karin E. Schütz

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āta mātai, mātai whetū

Contents

Executive Summary

- Heat stress in sheep is a global health, welfare and production issue that is likely to be exacerbated in future with predicted climate change.
- The thermoneutral zone of sheep is approximately between 5 and 25°C but depends on a range of environmental and individual factors.
- Heat load can be described by air temperature, Temperature-Humidity Indices (THI) and Heat Load Indices (HLI). Thresholds for when animals start to be affected by warm weather need to be established for sheep farmed in New Zealand conditions to protect their health and welfare.
- Heat stress is a major issue in predominantly tropical, sub-tropical and arid climates, however, research suggests that unshaded sheep in temperate regions, such as in most of New Zealand (northern parts experiencing sub-tropical conditions), are also likely to experience heat stress in summer.
- Heat stress increases respiration rate and body temperature, which in turn increases energy requirements for maintenance. When an animal is unable to lose sufficient heat through its cooling mechanisms, there is a reduction in feed consumption mainly to reduce heat production and reduce basal metabolism. This will negatively impact production.
- Heat stress can also result in mineral and hormonal imbalance, reduced immunity, impaired fertility and reproduction, effects on offspring and in extreme situations, death.
- Sheep will use shade in warm weather and access to shade improves the well-being of the animals by reducing respiration rate and body temperature. Shade reduced body temperature in sheep in New Zealand at air temperatures >20°C.
- Animal perceptions and affective states are important in welfare considerations, and more research is needed to assess the affective state of outdoor managed sheep in New Zealand.
- Similarly, more research around heat stress of sheep in New Zealand and associated mitigation strategies is encouraged.

1. Introduction

The foundations of the New Zealand sheep flock were imported from Australia and the United Kingdom in the early to mid-1800s (Johnson et al. 2021). Merinos were originally favoured because of the fine wool, however, when the ability to export meat was possible, dual-purpose sheep, capable of producing both meat and wool suitable for manufacturing, became increasingly popular. Through the early to mid-1900s new breeds were imported, predominantly from the United Kingdom and also breeds were developed within New Zealand to be better suited to the environment (Johnson et al. 2021). Three common breeds that continue to be farmed today are the Corriedale (Lincoln or Leicester x Merino), Perendale (Cheviot x Romney) and Coopworth (Border Leicester x Romney) (Johnson et al. 2021).

New Zealand sheep are predominantly managed outdoors in pastures with or without shade and shelter. Whereas the temperate climate in most of New Zealand (northern parts experiencing sub-tropical conditions) in general allows livestock to be managed outdoors, there are periods where inclement weather, both in winter and in summer, impose challenges to the welfare and productivity of animals. Concerns about effects of weather on farm animal welfare are constantly growing. Indeed, global warming is predicted to increase the frequency of heat waves and extreme weather events as well as global mean temperatures (Easterling et al. 2000, Meehl and Tebaldi 2004), indicating, for example, that the negative effects of heat stress are predicted to increase in future (Misztal 2017). Whereas new knowledge about animal responses to the environment continues to be developed, managing livestock to reduce the impact of climate remains a challenge. In particular, environmental management strategies are needed to guide managers when making decisions prior to and during periods of adverse weather. The identification of heat-stressed animals and understanding the biological mechanisms by which heat stress reduces production, reproductive functions and welfare is critical for developing novel approaches to maintain production, minimise the reduction in productivity and enhance sheep welfare during heat stress conditions. Since sheep are considered very resilient animals, their ability to cope with hot environmental conditions, without harming their welfare and productive performance, has often been overrated (Al-Dawood 2017). Improved understanding of the impact of heat stress will help in developing management techniques to alleviate heat stress in animals.

Heat stress is becoming an important constraint for animal production in many parts of the world. This review describes the effects of increased heat load and heat stress on the behaviour, physiology, health and production of sheep. It also includes a discussion about potential affective state of heat-stressed animals and mitigation strategies. It briefly touches upon effects on reproduction, cellular and immunological responses, and milk and meat quality. For a more thorough review of these areas see other review articles, for example by Al-Dawood (2017). Most of the research about heat stress in sheep originates from tropical, sub-tropical and arid regions, and there is very little information about heat stress in sheep in temperate regions. It is therefore difficult to currently quantify the magnitude of heat stress sheep in New Zealand may experience and any negative impacts on production and welfare. Limited research from New Zealand suggests that sheep are likely to experience heat stress in summer and with increasing temperatures and climate extremes, this is a welfare issue that is likely to increase in the future. The impacts of heat stress is a research area that needs more investigating, particularly in light of climate change. It is likely that increasing temperatures in future could lead to associated animal health and welfare issues, such as increased risk of external (e.g. flies) and internal parasites (e.g. Haemonchus), foot problems (e.g. footrot) and facial eczema (Johnson et al. 2021).

2. Effects of heat stress on the health, production and welfare of sheep managed on pasture

2.1 Heat load and heat stress

Sheep are homeothermic animals which means they can maintain near-constant body temperature (normal range for a sheep is 38.3–39.9°C) under a range of environmental conditions. The range of temperatures when the animal needs no additional energy to maintain its body temperature is called the thermoneutral zone (Kadzere et al. 2002). However, different authors have defined the thermoneutral zone and in particular the upper critical limit in varying ways (Silanikove 2000), which makes it hard to establish a uniform definition of the thermoneutral zone. For example, some reported the thermoneutral zone to be between 5 and 25°C (Curtis 1983) whereas Taylor (1992) reported it to be between 12-32°C. The true 'zone' will depend on a wide range of other environmental and animal factors, as discussed below in this review. In addition, most of the early work around thermoneutral zones was conducted in climate-controlled chambers, and it is doubtful whether these results are applicable to outdoor situations (Silanikove 2000). In general, it is considered that conditions below or above the thermal neutral range alter intake and metabolic activity (NRC 2001).

Thermoregulation is the mean by which an animal maintains its body temperature and it involves a balance between heat gain and heat loss and heat production. Excessive heat load or heat stress describes the situation where the thermoregulatory mechanisms fail to regulate the body temperature within its normal range (Joy et al. 2022) and when the amount of heat generated by an animal's body exceeds the ability of the body to distribute heat to its surroundings. When heat stress occurs depends on a number of environmental and animal factors. Environmental factors include air temperature, humidity, direct and indirect solar radiation and wind movements. Animal factors include for example, breed, age, sex, production level, fleece cover and health status. Heat stress is one of the most important stressors of ruminants especially in the tropical, subtropical, arid and semiarid regions of the world (Al-Dawood 2017).

The effects of heat stress on the health and biological functioning in sheep are well documented. Heat stress results in decreased growth, reproduction, milk quantity and quality, and natural immunity (Caroprese et al. 2008, Al-Dawood 2017) and changes in blood components and biological/biochemical pathways (Abdelnour et al. 2019). Heat stress can be divided into chronic and acute stress. In chronic heat stress, the elevation in temperature continues for a long period of time (days to weeks), allowing environmental acclimation. Acute heat stress means there is a rapid and brief increase in ambient temperature. Both types of heat stress stimulate physiochemical responses, such as depression of immune and endocrine functions (Abdelnour et al. 2019). In extreme conditions, prolonged heat stress can also lead to high morbidity, and mortality (Phillips, 2016). As mentioned earlier, the majority of the information about heat stress in sheep to date comes from very warm climates and there is limited information about heat stress of sheep in New Zealand.

2.2 Measures of heat load: the temperature-humidity index and heat load index

An animal's heat load can be measured in different ways, the most common being air temperature and the Temperature Humidity Index (THI). There are several different THI equations presented in the literature (reviewed by Seijan et al. 2017), most of these used dry bulb temperature (ambient temperature) and air moisture content. For example, Hahn (1997) estimated THI as follows:

$THI = 0.81\ db\ ºC + RH\ (db\ ºC - 14.4) + 46.4$

where db °C is the dry bulb temperature and RH is the relative humidity RH%/100.

Marai et al. (2007) suggested a THI to estimate the severity of heat stress in sheep, where T is the dry bulb temperature (°C) and RH is the relative humidity (%)/100:

$THI = T - (0.31 - 0.31 \times RH) \times (T - 14.4)$

These authors proposed four heat stress categories (Table 1). THI values and the corresponding air temperature and humidity levels are provided in Table 2.

Table 1. THI heat stress categories as described by Marai et al. (2007)

THI class	Heat-stress category
$THI < 22.2$	absence of heat-stress
$22.2 \leq THI < 23.3$	moderate heat-stress
$23.3 \leq THI < 25.6$	severe heat-stress
$THI \geq 25.6$	extreme severe heat-stress

Table 2. THI table showing moderate heat stress (yellow), severe heat stress (orange) and extreme severe heat stress (red) levels as suggested by Marai et al. (2007).

Air temperature (°C) \ Relative humidity (%)	0	10	20	30	40	50	60	70	80	90	100
20	18	18	19	19	19	19	19	19	20	20	20
21	19	19	19	20	20	20	20	20	21	21	21
22	20	20	20	20	21	21	21	21	22	22	22
23	20	21	21	21	21	22	22	22	22	23	23
24	21	21	22	22	22	23	23	23	23	24	24
25	22	22	22	23	23	23	24	24	24	25	25
26	22	23	23	23	24	24	25	25	25	26	26
27	23	23	24	24	25	25	25	26	26	27	27
28	24	24	25	25	25	26	26	27	27	28	28
29	24	25	25	26	26	27	27	28	28	29	29
30	25	26	26	27	27	28	28	29	29	30	30
31	26	26	27	27	28	28	29	29	30	30	31
32	27	27	28	28	29	29	30	30	31	31	32
33	27	28	28	29	30	30	31	31	32	32	33
34	28	29	29	30	30	31	32	32	33	33	34
35	29	29	30	31	31	32	32	33	34	34	35

It is well-known that the efficiency of evaporative cooling increases with increasing air velocity and decreasing relative humidity (Silanikove, 2000). However, the THI does not include the effects of solar radiation and wind speed and for this reason the Heat Load Index (HLI) was developed which is considered a more sensitive index, especially for animals living outdoors. The HLI was developed by Gaughan et al. (2008) for feedlot cattle and is based on behavioural responses and changes in dry matter intake. The HLI is based on relative humidity, wind speed and black globe temperature (radiant temperature) and consists of two parts based on a black globe threshold of 25°C:

HLI if BGT > 25 = 8.62 + (0.38 x RH) + (1.55 x BGT) + EXP(-WS + 2.4) – 0.5 x WS,
HLI if BGT < 25 = 10.66 + (0.28 x RH) + (1.3 x BGT) – WS)
Where T = air temperature (°C), RH = relative humidity (%), BGT = black globe temperature (°C) and WS = wind speed (m/s).

HLI has been used for sheep, for example by Mengistua et al. (2017), however, there is no literature describing the responses of New Zealand grazing sheep to different HLI.

2.3 Animal factors influencing susceptibility to heat load

Sheep are popular worldwide, due to their multipurpose ability to provide meat, milk and wool (Dwyer 2009). Also, sheep are well adapted to different geographical and environmental conditions including extreme and harsh climates (Al-Haidary et al. 2012). At a phenotypic and genotypic level, sheep breeds that have evolved under different conditions demonstrate a range of adaptive features, including coat characteristics (colour, hair length and density), pigmented skin, fat tail shape, heat and drought tolerance. Around the world, there are more than 1,000 sheep breeds (Dwyer 2009) and these breeds differ in their capacity to overcome climatic conditions.

The physical structure of the coat is the first layer between the body and the environment. Several coat characteristics are directly related to heat loss or gain from the environment and the hair structure can protect the skin against direct solar radiation and promote convection and heat loss by evaporation (McManus et al. 2020). The level of protection varies according to coat colour, depth and length (Silanikove 2000, McManus et al. 2020). Wool acts as a protective barrier but also makes evaporation of water from the skin more difficult, thus reducing the ability to lose heat through sweating (McManus et al. 2020). In general, shorn sheep seem to tolerate high temperatures better than unshorn sheep (Marai et al. 2007, Beatty et al. 2008), however, there may exist an interaction with humidity; it has been suggested that shorn sheep tolerate hot-humid conditions better than fleeced sheep, whilst fleeced sheep have improved tolerance to hot-dry conditions (Beatty et al. 2008). This is likely due to wool cover decreasing the sweating ability of sheep. The effects of wool coverage on water turnover in relation to thermoregulation in sheep were investigated by Al-Ramamneh et al. (2011). Those authors found that even under temperate conditions (<28°C) shearing (compared with wool length of 10.6cm) reduced core body temperature (39.3 vs. 38.8°C), surface temperature (body side: 19.3 vs. 24.5°C; leg: 25.8 vs. 27.4°C), water intake (165 vs. 134 $g \cdot kg^{-0.75} \cdot d^{-1}$) respiration rate (66 vs. 31 breath/min) and increased dry matter intake (52 vs. 59 $g \cdot kg^{-0.75} \cdot d^{-1}$) in German Blackhead mutton sheep, thus indicating that unshorn sheep are likely to experience heat stress also in temperate conditions.

Morphological traits seem to affect heat tolerance, for example, haired sheep usually tolerate heat better than woolly sheep especially in tropical climates with high temperature and high humidity (McManus et al. 2009). However, McManus et al. (2020) suggested that it is the adaptation to hot environments and not the type of coat (wool vs hair) itself that determines the capacity of the resistance of the animals to heat stress, due to modifications in essential pathways such as energy metabolism, physiological responses and body size. The heat stress tolerance of breeds that are common in New Zealand should be assessed under New Zealand conditions to evaluate their suitability to different regions and also in light of climate change.

Animals with a dark coat have greater absorption of thermal radiation and are in general more susceptible to heat stress than those with a lighter coat colour (Silanikove 2000, McManus et al. 2020). Body size and composition may be important to heat stress adaptation, but the literature is mixed. It has been suggested that smaller body size is an adaptation to warmer climates, however, larger animals have lower metabolic rates so would gain heat at a slower rate (McManus et al. 2020). It has also been suggested that tall animals with long, thin appendages reduce heat gain and increase heat loss as these characteristics are often observed in desert ungulates (McManus et al. 2020). There are also other adaptations, for example, in indigenous sheep breeds from arid and semi-arid regions, the external localisation of the fat in the tail allows better heat dissipation from the rest of the body since the body becomes less insulated by the fat tissue (Degen and Shkolnik 1978).

2.4 Animal responses to increased heat load

Sheep respond to increased heat load using a range of behavioural, biochemical and physiological processes to maintain normal body temperature (Silanikove 1992, Marai et al. 2007). Most of the adjustments made by an animal involve dissipating heat to the environment and reducing the production of metabolic heat (Silanikove 2000), however, avoiding gaining heat from the environment is also important (Figure 1). Hyperthermia during exposure to heat stress is the result of the decreased thermal gradient between the animal and the surrounding environment, and as a result sensible heat loss (i.e. convection, conduction and radiation) becomes less effective (Al-Haidary 2004). Under such conditions animals depend on evaporative cooling mechanisms from their skin and respiratory tract. Animals will modify their behaviour to avoid gaining heat from the environment, such as seeking shade. However, if unable to do so, or if conditions become too extreme, heat stress may lead to drastic changes, e.g. a decrease in feed intake efficiency and utilisation, disturbances in water, protein, energy and mineral balances, enzymatic reactions, hormonal secretions and blood metabolites, reduction in fecal and urinary water losses and an increase in sweating (limited in sheep due to wool cover), respiration and panting and heart rate (Al-Dawood 2017, Figure 2). Some of these changes are discussed in more detail below.

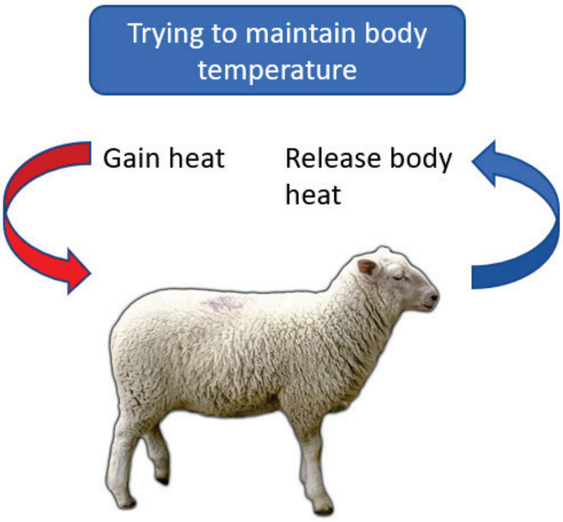

Figure 1. Sheep try to maintain normal body temperature by avoiding gaining heat from the environment and by releasing excess body heat. They use several behavioural and physiological mechanisms to do this.

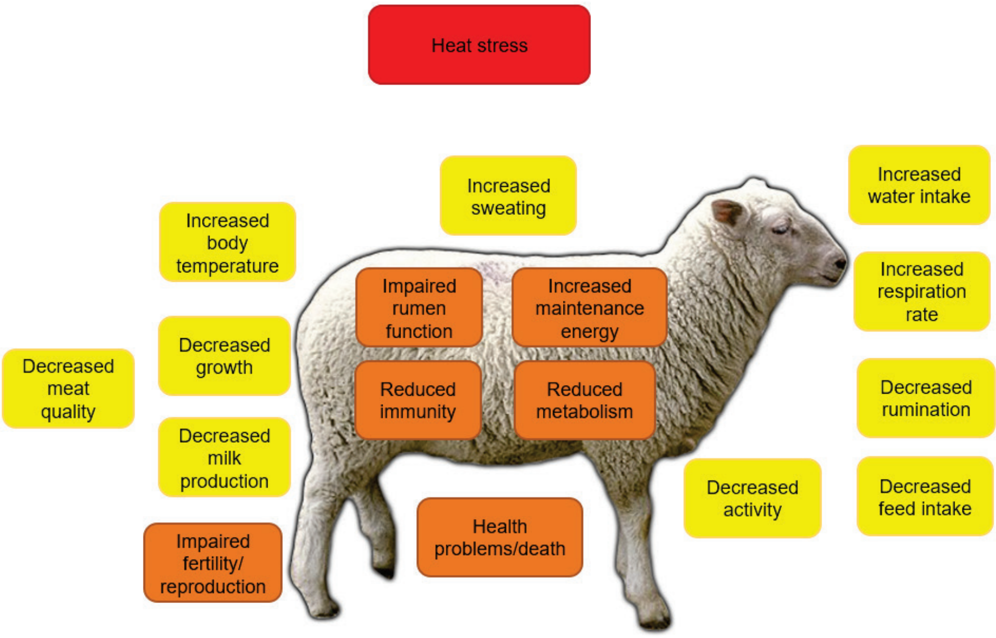

Figure 2. Sheep responses to heat stress. Yellow boxes indicate visible signs of heat stress. Orange boxes indicate invisible consequences of heat stress.

2.4.1 Behaviour

Animals will change their behaviour to avoid gaining radiated heat from the environment and increase heat loss via convection and conduction. Behavioural responses of sheep include seeking shade and crowding (Silanikove 2000), panting, open-mouth breathing, decreasing feeding behaviour (Caroprese 2008) and rumination (Hirayama et al. 2000), and increasing water consumption (Caroprese 2008) and time spent near water (Thomas et al. 2008). There is also a change in body posture (increased standing, Bligh 1985) and orientation towards the sun if there is no shade available. Sheep may utilise different areas in paddocks on cold (<23.2°C) vs. hot days (>26°C) and adjust distance travelled and distances to water troughs, likely to manage heat load by staying close to drinking water, reduce activity and conserve energy (Thomas et al. 2008). A change in diurnal behavioural patterns (Dwyer 2009) where animals are more active during the night when it is cooler has also been observed.

Like other ruminants, one of the early behavioural responses to warm weather includes seeking protection from solar radiation (Sherwin and Johnson 1987) and this response is evident also in temperate climates. In New Zealand, Romney crossbred ewes spent differing amounts of time in shade (43% and 67% of daytime observations, respectively) depending on if conditions were warm and dry (Otago; mean daily temperature 18.5°C, humidity 49%), or warm and humid (Waikato; mean daily temperature 22.0°C, humidity 67%, Pollard et al. 2004). Daytime grazing was reduced in warm weather at both sites (total grazing was not measured, Pollard et al. 2004). Indeed, there seems to exist a change in activity in warm conditions with a general decrease in grazing and a change in lying time which may potentially be dependent on air humidity levels. Pollard et al. (2004) demonstrated that grazing behaviour decreased with increasing air temperature in the Waikato and sheep without shade spent less time lying compared to sheep with access to shade, which is consistent with the findings of Lowe et al. (2002). In contrast, with increasing temperatures in Otago (lower humidity), both sheep with and without shade increased their lying activity and reduced grazing activities (Pollard et al. 2004). Merino sheep in the Mackenzie country in the South Island, which also has a dry climate, also increased their lying activity and reduced grazing activities (Scott and Sutherland 1981). Increased standing could be a strategy to allow for more air flow and therefore convective cooling around the body. In the absence of shade it has been observed that sheep form small, tight groups and tend to hold their heads in the shade provided by the bodies of other sheep (Scott and Sutherland 1981, Gregory 1995). This crowding or grouping behaviour can be a thermal response but may also be an insect avoidance response (Mooring et al. 2003).

2.4.2 Physiology and Immune function

Physiological responses are critical to maintain normal body temperature and to prevent hyperthermia. Respiration rate, core body temperature and heart rate have often been used as indicators of physiological adaptability to heat stress in small ruminants (Al-

Dawood 2017). Sheep dissipate excess body heat by sweating and increasing respiration rate/panting (Marai et al. 2007) with heat dissipation via legs and ears increasing in very high air temperatures (36°C). Respiration rate (breaths/min) increases heat dissipation through increasing respiratory evaporation and changes quickly in response to both animal activity and heat load. It is therefore a commonly used indicator of heat stress. Normal respiration rate in sheep range from 16 to 30 breaths/min (Zaytsev et al. 1971) and under neutral environmental temperature (12°C), sheep lose about 20% of their total body heat through respiration; this rate increases by about 60% at an ambient temperature of 35°C (Thompson 1985). Silanikove (2000) categorised heat stress in sheep as low: 40-60, medium: 60-80, high 80-120 and severe:>200 breaths/min. Maximum values of about 300 breaths/minute have been reported (Hales and Brown 1974, Lowe et al., 2002). This maximal respiration rate was associated with rectal temperatures of 39.8˚C (Hales and Brown 1974) and 40.5˚C (Lowe et al. 2002). Beyond this maximal value breathing becomes slower and deeper and leads to respiratory alkalosis (Hales and Brown 1974, Lowe et al. 2002). In New Zealand, Pollard et al. (2004) reported respiration rates of 121 breaths/min and 226 breaths/min in dry (Otago) and humid (Waikato) conditions, respectively, which would put them into the category of high to severe levels of heat stress following the Silanikove (2000) categorisation.

In combination with respiration rate, the panting characteristics, such as breathing with an open mouth and protruding tongue can be used as reliable indicators of heat stress. A panting score index for sheep (ranging from 0 to 4) has been developed by Lees et al. (2019) and is similar to one developed for cattle. Those authors demonstrated a strong relationship between respiration rate and panting score. Contrasting with other ruminants where sweating plays a key role to avoid hyperthermia, sheep may dissipate between 60 and 90% of the total heat load by increasing respiratory rate, and less than 10% by sweating (Marai et al. 2007). Sheep are considered intermediate between horses and cattle (species in which sweating prevails) and pigs (in which panting is the main pathway for heat dissipation) with regard to the importance of sweating in thermoregulation (Hörnicke 1987). However, in a fully fleeced sheep, evaporation of sweat or body water from the skin is hindered because a fleece contains air spaces with water vapour, which is in equilibrium with the water either absorbed or adsorbed on the wool fibres (Gatenby et al. 1983). Evaporative cooling via panting, has been reported to amount to 65% of the total heat loss in fleeced sheep and 59% of the total heat loss in shorn sheep (Hofman and Riegle 1977, Beatty et al. 2008).

Like respiration rate, an animal's heart rate (beats/min) changes rapidly depending on the animal's biological activities or by external factors such as temperature. Higher pulse rates help in heat loss by increasing blood flow to their body surface which will lead to higher skin temperature (Marai et al. 2007) due to the vasodilatation of skin capillaries to enhance the blood flow. Normal heart rates have been reported to range from 70 to 80 beats/min for sheep (Zaytsev et al. 1971), however, the literature regarding heart rate and heat stress is mixed. Some authors have reported an increase in warm conditions (83 beats/min: Al-Haidary et al. 2012; 90 to 107 beats/min: Wojtas et al. 2014), however, some have reported a reduction in the daily average heart rate in sheep (from 115.7 to 85.8 beats/min: Al-Haidary 2004). In contrast, Sunagawa et al. (2002) did not detect any significant changes in heart rate when sheep were exposed to heat stress. It has been suggested that reduced heart rate may reflect reduced metabolic rate (Barkai et al. 2002), which is an adaptation to warm conditions to reduce heat load and maintain normal body temperature (Al-Haidary 2004).

Normal body temperature for sheep ranges between 38.3–39.9°C (Heath and Olusanya 1985, Marai et al. 2007, Okoruwa 2015). When physiological and behavioural mechanisms fail to mitigate excessive heat load, the body temperature will rise and result in dramatic changes in biological function. For example, an increase in body temperature is associated with a marked reduction in feed intake, redistribution in blood flow and changes in endocrine functions that will negatively affect productive and reproductive performance (Eltawil and Narendran 1990). The core body temperature is therefore a good indicator of the thermal balance and heat stress (West 1999). If rectal temperature exceeds 41.7°C, death may occur as the animal cells begin to degenerate (Thwaites 1985, Marai et al. 2007).

Hormones are important in thermoregulation and metabolic adjustments in animals, particularly those produced from the pituitary (prolactin), adrenal (cortisol) and thyroid glands (Triiodothyronine—T3 and Thyroxine—T4). Stress hormones, produced in response to an increase in environmental temperature, induce mobilisation of energy, primarily, for maintenance of muscular and neural functions. The activation of the hypothalamic-pituitary-adrenal axis (HPA axis) may lead to enhanced production of corticotropin-releasing hormone (CRH) in the hypothalamus, which stimulates adrenocorticotropic hormone (ACTH) from the anterior pituitary, in turn causing increased cortisol (a stress hormone) secretion from the adrenals (Engler et al. 1989). Not all studies in small ruminants, however, show elevation of plasma levels of cortisol (Joy et al. 2020a) and therefore, cortisol may not be a reliable indicator of heat stress. Prolactin is involved in water conservation, sweat gland activity and is elevated in hot conditions (Joy et al. 2020a). Depressed thyroid activity is another result of heat stress in small ruminants, accounting for lower metabolic activity, reduced rumen motility and decreased feed transit through the digestive tract (Joy et al. 2020a).

There is also an overall negative relationship between stress and immune response. Exposure to stressful environmental conditions can influence the immune system, mainly through the release of immunosuppressant hormones, such as glucocorticoids (Chedid et al. 2014, Chauhan et al. 2014, 2021). The effect of heat stress on sheep immunity, milk production as well as udder health was reviewed by Sevi and Caroprese (2012); those authors suggested that heat stress reduced cellular immunity by decreasing cellular proliferation. The mechanism of action, however, is unclear and may involve heat shock proteins, altered cytokines profiles as well as changing cortisol levels. Sevi et al. (2009) reported a drastic drop in immunity in ewes exposed to high ambient temperatures; the reduction in immune function was associated with a significant mineral imbalance and an increase in milk neutrophil levels, and higher counts of Staphylococci, coliforms and Pseudomonas, thus showing how heat stress can negatively influence both the health and milk quality of sheep.

In addition, the biochemical profile of ruminants is also modified under hot environments, with changes in hematocrit values, hemoglobin and lowered blood levels of glucose, protein, cholesterol and non-esterified fatty acids (NEFA) (Das et al. 2016).

2.4.3 Feed intake and production

There is a well-known reduction in feed intake by ruminants in warm conditions (West 1999). Reductions in feed intake, and subsequent body weight and daily gain has been reported in sheep in several studies and several breeds (Nardone et al. 1991, Kandemir et al. 2013, Marai et al. 2007). For example, heat stress reduced feed intake in second-cross Merino (Poll Dorset x Merino/Border Leicester) lambs, but not Dorper lambs when both breeds were subjected to heat stress (Joy et al. 2020b). In this study, the Dorper lambs also had lower respiration rate, rectal temperatures and skin temperatures than the second-cross Merinos. The daily feed intake and feed conversion decreased in Suffolk lambs under hot conditions in a climatic chamber (30.5°C) compared to a group under shelter (19.3°C) in spring (Padua et al. 1997).

The reduction in feed intake is an attempt to generate less metabolic heat due to heat production associated with feeding (Kadzere et al. 2002). The reduction in feed intake could also be due to a reduction of feed transit through the digestive tract (increased gut fill and depressed intake, Rana et al. 2014), a decrease in blood flow to the rumen and a reduction in both ruminal motility and rumination (da Costa et al. 1992), and also due to direct effects on the hypothalamus resulting in decreased metabolic rate and body weight (West 1999). During heat stress, there is a reduction in the amount of saliva produced and salivary HCO3 − content, which may impair rumen functionality (Kadzere et al. 2002). Heat stress is associated with an increase in maintenance requirements (NRC 2007) which is partly due to higher respiration rates (Sevi and Caroprese 2012), which might mean that heat-stressed animals may be in a negative energy balance (Moore et al. 2005), which in turn is likely to result in some of the negative effects we see on production, health and reproduction.

Heat stress affects meat quality, carcass characteristics and the organoleptic quality of sheep (Al-Dawood 2017). The degradation of meat quality variables (pH, colour, texture and moisture) is referred to as dark cutting or dark-firm dry, high pH, low glycogen meat (Schaefer et al. 1997). Sheep and goats slaughtered under an ambient temperature of approximately 35°C had a higher pH (5.78 vs. 5.65) level and myofibrillar fragmentation index in muscles, which is an indicator of the extent of myofibrillar protein degradation of meat post-slaughter (86.9 vs. 85.6%), lower colour, and expressed less juice than those slaughtered at 21°C (Kadim et al. 2008), thus indicating that seasonal temperatures were the main reasons for differences in meat quality. In addition, Rana et al. (2014) reported that meat quality of sheep was negatively affected at 28°C, 82% humidity; drip loss increased more in the control group and differences were found in the weight of the heart, kidney, lung and trachea between control and heat exposed groups. Higher incidence of high ultimate pH and dark firm and dry (DFD) meat or no impacts of heat stress have been reported in sheep and cattle as reviewed by Zhang et al. (2020).

The reduction in quantity and quality of milk is a well-known and costly negative effect of heat stress in dairy animals. This review mainly focuses on non-dairy sheep and any potential effects on milk production is therefore not further discussed, however, there is a need for research around heat stress in New Zealand dairy sheep and the effects on their health, production and welfare. It is worth noting that milk production (and therefore their maternal production ability) of New Zealand ewes with lambs at foot may be affected by warm weather depending on when the warm weather occurs, however, this has not been described in the literature. In general, heat stress decreases milk production including fat and protein (Finocchiaro et al. 2005).

2.4.4 Water intake

Water is essential to life and one of the most important nutrients. It is critical for the regulation of body temperature, growth, reproduction, lactation, digestion, nutrient exchanges and transport in blood, excretion of waste products and heat balance (Al-

Dawood 2017). Severe water deprivation in sheep can result in physiological changes, weight loss and death and highly depends on the conditions and the breed of sheep (Al-Dawood 2017).

There is a positive relationship between feed intake and water intake (Silanikove 1992) and situations where water is limited is likely to influence the animals negatively in terms of both welfare and productivity. Water intake of animals depends on several environmental and individual factors, such as ambient temperature, dry matter intake, loss of water from evaporation, urine, faeces, and milk (Al-Dawood 2017). Marai et al. (2007) reported a water intake increase of 50%, and a water loss decrease of 25% in the faeces and 40% in urine, during heat stress. Corriedale ewes consumed 4.2 L of water per day at 25-30°C and 76-88% humidity (Ghassemi Nejad et al. 2014). The water intake increased in warm weather (Ghassemi Nejad et al. 2014) which is in accordance with other studies (Ismail et al. 1995, Marai et al. 2007). Indeed, sheep consumed 2 kg of water/kg dry matter at air temperatures between 0 and 15°C, and this ratio increased threefold at temperatures above 20°C (Conrad 1985). Water intake of sheep (Skudde breed) grazing pasture increased with temperature and humidity in a temperate climate (mean temperature was 15-16°C, max temperature was 21-22°C, Fischer et al. 2017). In this study, the water consumption of lactating ewes varied between 41 and 77 mL /(kg $W^{0.75}$) which corresponded to 0.5–1.0 L/sheep/day. After the lambs were removed, from July to September, the adult sheep drank 10–62 mL/(kg $W^{0.75}$) (0.1–0.9 L/sheep/day). In October, at the start of pregnancy, these sheep consumed only 9–18 mL/ (kg $W^{0.75}$) (0.1–0.2 L/sheep/day) of water (Fischer et al. 2017). Unshaded sheep drink more water than shaded sheep; the sheep in the New Zealand study by Pollard et al. (2004) consumed on average, 3.5 L water per day if they were unshaded, and on average. 2.95 L/d when shaded in summer in the Waikato. In agreement with this, in a South African study, ewes in non-shaded paddocks drank 26% more water than ewes in paddocks with shade (Cloete et al. 2000).

Similar to cattle, sheep seem to prefer to drink water that has a temperature that is close to ambient temperature (Savage et al. 2008), however, there is evidence that providing cooler drinking water in very hot climates can reduce the negative effects of heat stress; rams provided with cooler water (24-28°C) had lower losses in body weight and improved metabolic activity compared to rams with drinking water of ambient temperature (38-44°C, De et al. 2020).

2.4.5 Reproduction

Heat stress is a major factor in lowering the fertility of livestock that are mated in summer and reproductive issues in relation to heat stress are particularly severe in tropical and sub-tropical regions (Marai et al. 2007). There are two mechanisms by which heat stress leads to infertility in animals, the direct effect of hyperthermia and HPA activation on the reproductive axis or indirect effect of heat stress on feed intake in order to reduce metabolic heat production leading to changes in energy balance and nutrient availability. These changes act via the Hypothalamic-hypophyseal axis and cause negative effects on reproductive performance (McManus et al. 2020). Heat stress can affect all stages of reproduction in females including a suppressive effect on reproductive hormones (McManus et al. 2020). Heat stress reduces fertility, ovulation, expression of estrus, conception rate, embryonic survival and fetus development as well as follicular and oocyte development (McManus et al. 2020). Pregnant and lactating ruminants are more susceptible to heat stress compared to non-pregnant and non-lactating animals due to higher energy demands in those animals (McManus et al. 2020). In addition, lactating animals produce a lot of metabolic heat which makes them more susceptible to heat stress (Hansen 2009). In a review and meta-analysis article by Romo-Barron et al. (2019) it was reported that heat stress decreased the duration of estrus in cycling ewes but increased the length of the cycle. Heat-stressed cycling ewes had greater odds of embryo mortality and a decreased chance of impregnation. In addition, pregnant ewes which were heat-stressed had reduced placental and fetal weights (Romo-Barron et al. 2019), which suggests a negative effect of heat stress also on the offspring. Furthermore, thermoregulation ability in newborn lambs can be influenced by the environmental temperature the mothers were exposed to during pregnancy (Stott and Slee 1985).

In males, heat stress impairs sperm production and motility, and increases the proportion of morphologically abnormal spermatozoa, thus affecting semen quality (Hansen 2009), which may be of practical importance in New Zealand (Gregory 1995). Heat stress in males may also affect sexual behaviour and reduce sexual activity (Dwyer 2009). In a review article van Wettere et al. (2021) concluded that both ewe and ram reproduction is affected by relatively modest levels of heat stress.

2.5 Heat stress and affective state

Societal concerns around animal welfare can be divided into three overlapping categories: 1) biological functioning, meaning that animals should function well in the sense of good health, and normal growth and development, 2) affective state, which describes how the animal is feeling, and 3) naturalness, meaning that animals should have the ability to express normal behaviour that they are strongly motivated to do in an environment with some natural elements (Fraser 2008, Figure 3). Physical function (e.g. health and production) and negative affective states (e.g. pain and hunger) have historically been the main focus in welfare assessments. It is now, however, generally agreed that welfare assessments also need to take into consideration positive affective states, such as pleasure or being content, and the ability to perform behaviours that are important to the animals. This was reflected in an amendment in 2015 of the New Zealand Animal Welfare Act to include a statement that all animals are considered sentient, which means they can have positive and negative experiences and emotions. While it is still uncertain what this means to the animal industries in New Zealand, the research area of animals' affective state is gaining increasing attention worldwide. For example, a recent review article discussed the potential underlying affective state of heat-stressed cows (Polsky and von Keyserlingk 2017). When animals lose the ability to control their environment (e.g. the need for shade to reduce body temperature or the need for water to alleviate dehydration), there are associated risks to the animal's welfare that may not necessarily be linked to direct biological functioning. For example, insufficient access to shade or water in dairy cattle results in increased aggression due to competition (Schütz et al. 2010), which may lead to frustration. Polsky and von Keyserlingk (2017) suggested that a broader approach to heat stress is required, that includes how heat stress may cause negative affective states, in addition to negative physical consequences, and that heat mitigation strategies should, where possible, consider the natural adaptations of cows to aversive conditions. Whereas the effects of heat stress on the biological or physical functioning of sheep have been thoroughly researched and described in the literature, less is known about other aspects of welfare, specifically affective state and natural living. Cockram (2004) was comparing the increased respiration rate seen in sheep in warm weather with that of humans and suggested that, by analogy, it would not be unreasonable to propose that the increased respiration rate shown by sheep when exposed to high environmental temperatures could be associated with an aversive emotional response, similar to that of humans. It is encouraged that more research in these areas is undertaken.

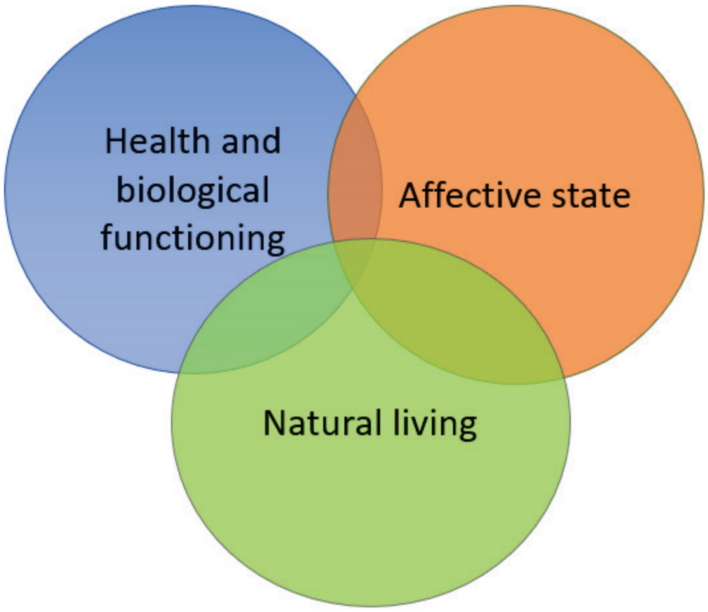

Figure 3. Ethical concerns around animal welfare. Modified after Fraser et al. (1997)

2.6 Heat stress mitigation

Heat stress amelioration strategies can be broadly grouped into three categories: modifying the environment, management including nutritional modifications, and genetics and breeding (Morrison 1983).

2.6.1 Modifying the environment

Even though cooling with water is effective in reducing respiration rate and body temperature in sheep (Darcan et al. 2007) this is not a practical strategy in pasture-based systems, such as New Zealand. Instead, in such systems, providing natural or man-made shade is an economical management strategy that efficiently protects the animals from direct solar radiation (Silanikove 2000). It has been estimated that a well-designed shade structure can reduce the heat load by up to 50% (Muller et al. 1994). Silanikove (2000) suggested that shade was essential to the welfare of farm animals in areas where ambient temperatures typically exceed 24˚C and the THI exceeds 70. The provision of shade to sheep and goats has been shown to improve weight gain, milk production and reproductive performance (Berger et al. 2004).

From a welfare perspective, having access to shade in pastures allows the animals to choose when to use the resource, and to control their thermoregulation. In New Zealand, Romney crossbred ewes spent 43% and 67% of daytime observations, respectively in shade depending on if conditions were warm and dry (Otago; mean daily temperature

18.5°C, humidity 49%), or warm and humid (Waikato; mean daily temperature 22.0°C, humidity 67%). Sheep that had access to shade had lower body temperature and respiration rates at both locations and shade was efficient in reducing body temperature at temperatures >20°C (Pollard et al. 2004). In Estonia, which has a temperate climate, respiration rates correlated positively with panting scores in two groups of sheep (Estonian Whiteface sheep, wool length was 10-12 cm), one with and one without shade in summer (Marcone et al. 2021). Unshaded sheep had higher respiration rates and breathing intensity than shaded sheep, and open mouth breathing with tongue extended was only observed in the unshaded group. In addition, unshaded sheep were standing more and ruminating less than the shaded animals. In this study shade use increased with air temperature (Marcone et al. 2021) and it was concluded that unshaded sheep experienced heat stress even at temperatures less than 25°C. In an arid region in Australia Merino sheep (mean wool length was 19.8mm) spent more time in the shade and near water and reduced activity during periods of heat waves; the sheep spent on average 14.7 times longer in the shade during the midday than during typical non-heatwave periods (Leu et al. 2021). Shade use during heat waves was positively related with body condition change; sheep that used the shade more had better body condition at the end of the study (Leu et al. 2021) and the authors suggested that since body condition affects reproductive success, access to shade in warm weather may have positive flow-on effects on reproductive benefits. Provision of shade was also beneficial in terms of helping lactating ewes (Comisana ewes in late lactation in the Mediterranean) to minimise the adverse effects of high ambient temperature on thermal balance and energy and mineral metabolism (Sevi et al. 2001).

2.6.2 Management

Sheep demonstrate a shift in diurnal feeding activity to feed more during the cooler parts of the day (West 1999, Dwyer 2009) and changing feeding times as well as the changing the diet have been used to reduce heat load in sheep in very warm climates. These adjustments may include changes in feeding times and frequencies, grazing time, and ration composition such as dietary fiber adjustment, the use of high -quality fiber forage, increased energy density and use of feed additives (e.g. buffers (sodium bicarbonate), niacin, antioxidants (vitamin E and Se) and yeast culture) (Sevi and Caroprese 2012, Al-Dawood 2017). Supplementing heat-stressed sheep with betaine improved thermoregulatory responses by maintaining lower respiration rates, rectal temperature, skin temperature, and heart rate compared to animals fed with normal ration (DiGiacomo et al. 2016). Feeding diets with high roughage increased heat stress (increased respiration rate, heart rate and rectal temperature, and decreased feed intake and utlisation) in warm weather in Awassi wethers (Bhattacharya and Hussain 1974). Sevi et al. (2001) studied the cellular immune reactivity in sheep exposed to or protected from solar radiation and fed in the morning or in the afternoon. Those authors demonstrated a reduced in vivo lymphocyte proliferation in ewes exposed to solar radiation and in shaded ewes fed in the morning. These results suggest that both protection from solar radiation and changing feeding time to the afternoon can minimise the impact of thermal stress on ewe immune status by enhancing cellular immune response. In grazing systems, sheep are able to change their diurnal patterns of grazing themselves, however, there is no research that has been undertaken to describe diurnal patterns of grazing in New Zealand sheep in response to warm weather.

As the requirements for drinking water increase in warm weather, it is critical to provide sufficient high-quality, palatable drinking water to all animals in summer (Silanikove 2000). In addition, as forced activity and stress associated with handling and transportation increase the heat generated by the animals, these management practices are best to be avoided in warm weather (Al-Dawood 2017).

2.6.3 Breeding

Appropriate breed selection is a very valuable tool for sustaining animal production in increasingly challenging environments (Silanikove 1992). Selection of animals for thermotolerance is one viable strategy that exploits natural variation within and between breeds for desirable traits. The various biological markers used to improve thermotolerance in small ruminants include behavioural (feed intake, water intake), physiological (respiration rate, rectal temperature, sweating rate), hormonal (T3, T4 and growth hormone) responses and the response of molecular regulators (Joy et al. 2020a). There is a general antagonistic relationship between resilience and production, however, not considering resilience in breeding programs could lead to major production losses in future climate scenarios. For example, it was suggested by Ramón et al. (2021) that a selection weight of 20% for sheep resilience resulted in the best overall genetic response in terms of both production and resilience in Mediterranean climates. Thus, the selection of heat-tolerant animals from high-producing breeds helps these animals to keep high productivity under heat stress periods (Abdelnour et al. 2019). In addition, lambs born from ewes of the same flock and breed, which were able to maintain low rectal temperature have higher birth weight than lambs born from ewes with higher rectal temperature, suggesting that selection of ewes which can maintain normal rectal temperatures during periods of heat stress would produce lambs of normal birthweight in a hot climate (McCrabb et al. 1993).

Of the above-mentioned heat stress mitigation strategies, the provision of shade and clean, palatable drinking water is likely the most critical ones for New Zealand pastured sheep, however, diets could be modified to have a low heat increment in relation to energy provided for production. There should also be a consideration of what breeds are used; they need to be chosen to be resilient in New Zealand farming systems and also taking into account future changes in climate with the associated health and welfare risks, such as parasite load and disease.

3. Conclusions

Heat stress in sheep is a global issue which significantly impacts their welfare, health and productivity. Whereas heat stress is considered more of a challenge in tropical, sub-tropical and arid climates, there is limited research suggesting that sheep may experience heat stress and benefit from shade also in New Zealand which has a mix of temperate and sub-tropical regions. The majority of literature to date has focussed mainly on production, physiology, biochemical and reproduction effects of heat stress and more research is needed about how the animals experience warm weather and increased heat load to appropriately assess their welfare. In addition, there are only a few studies that have been undertaken in New Zealand that investigates heat stress in sheep. Mitigation strategies to alleviate heat stress include modifying the environment, management and breeding and all three strategies should be further investigated to improve the welfare of pastured sheep in a changing climate in New Zealand.

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