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Chronic stress in sheep: assessment tools and their use in different management conditions

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Abstract

Chronic stress occurs when animals are unable to deal with a persistent stressor with species-typical responses, or when several stressors are present concurrently. Chronic stress is most frequently considered in intensive systems, but it may also be a welfare concern for extensively managed species, such as the sheep. Here we review behavioural and physiological responses of sheep to experimentally induced chronic stressors to determine relevant indicators of chronic stress. Neuroendocrine responses to chronic stress are difficult to interpret because initial responses are followed by an apparent normalisation. Thus, cortisol or catecholamines may be at or below pre-stress levels during chronic stress, but this varies with different stressors. Chronic stress can also affect reproductive function, impair body and wool growth and meat quality, reduce immune function, and is associated with greater parasite burdens in sheep. Chronic stress induces alterations in behaviour patterns, particularly activity and feeding, and circadian rhythms of behaviour. Stereotypic behaviours, however, are infrequent in sheep and may occur only in experimental conditions of social isolation. Behavioural and physiological data suggest that rough handling and sheepdogs may be sources of chronic stress for sheep. Social subordination and weaning also act as chronic stressors, leading to higher parasitism in these animals and a greater response to additional stressors. Lameness and parasitism are associated with physiological and behavioural responses indicating that these are severe forms of chronic stress in sheep. It is unclear whether environmental stressors, such as weather and food availability, induce chronic stress in sheep. Under-nutrition may, however, be a welfare concern through its impact on lamb survival. The existence of many sources of chronic stress in the management of sheep suggests that the welfare of this species requires more attention than it has currently received.

Keywords: *animal welfare, behaviour, chronic stress, handling, lameness, parasitism, sheep*

Introduction

Stress can either be acute or chronic. Acutely stressful events either persist for a short duration or the animal has behavioural and physiological mechanisms to deal with the stressor or remove itself from it, and hence reduce its impact. In domestic animals, constraints of housing or other management practices may make it impossible for the animal to deal appropriately with a stressor. Retreat or escape may be impossible, normal behavioural routines may not be able to be performed or may be superfluous (Wiepkema & Koolhaas 1993). Under conditions where the animal is unable to deal appropriately with the stress event using species-typical behaviours or adaptations, and thus the stressful condition persists, or where multiple acute stressors are present either concurrently or consecutively, the animal is likely to experience chronic stress. Since the inability to perform natural behaviours is perceived as an important chronic stressor, attention has tended to focus on intensively husbanded animals, whereas chronic stress in more extensively managed animals, such as the sheep, has received less attention. However, these animals may still be kept in ways that restrict the expression of natural behaviours and may also experience, for example, conditions of under-nutrition, chronic lameness, parasitism and handling stress — sometimes simultaneously. For on-farm assessments of sheep welfare, it is important to know how sheep respond to conditions of chronic stress, since the presence of chronic stress will indicate poor welfare. This review examines the behavioural and physiological responses of sheep to experimentally induced chronic stress, and considers their use as tools to assess animal welfare and their use in on-farm conditions where chronic stress may occur. Although neuroendocrine parameters do not usually form part of on-farm assessments, they will also be considered briefly to provide a framework for assessing chronic stress.

1. Assessment tools to recognise chronic stress

Neuroendocrine responses to chronic stress in sheep

In general, stressors elicit a transitory rise in plasma glucocorticoids and catecholamines. However, under chronic stress, both the hypothalamic–pituitary–adrenal (HPA) system and the sympathetic–adrenal–medullary (SAM) system adapt to repeated or long-term exposure to a particular stressor. This differs from the classic and adaptive

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habituation, where the animal learns not to respond on repeated exposure to a harmless stimulus, as it is not inevitably accompanied by behavioural change (Jensen *et al* 1996). The process is more akin to a biochemical down-regulation of areas of the HPA response rather than a psychological adaptation, and is achieved by alteration of the control systems for stress responses (Jensen *et al* 1996; Terlouw *et al* 1997). This is believed to help the animal maintain sensitivity to further acute stressors or disease under conditions of chronic stress.

Social isolation of sheep on consecutive days elevates cortisol on each occasion (Niezgoda *et al* 1987; Minton *et al* 1992; Apple *et al* 1993), and normalisation to baseline values does not occur until after 9 h of isolation (Cockram *et al* 1994). Moving sheep indoors from pasture causes raised plasma cortisol that takes several weeks to normalise (McNatty & Young 1973; Pearson & Mellor 1976), whereas elevated cortisol levels in lambs following tail docking normalises after three days (Rhodes *et al* 1994). However, exposure to a random array of auditory stimuli causing elevated cortisol, resulted in no adaptation or normalisation of plasma cortisol after 24 days (Harlow *et al* 1987). Thus, with chronic stress, the time course of normalisation of HPA axis functioning in sheep varies from days to weeks depending on the stressor. With prolonged chronic stress, such as confinement in metabolism crates or severe lameness, cortisol is depressed below baseline values (Fordham *et al* 1991; Ley *et al* 1991a). Prolonged stress can also alter the circadian rhythm of cortisol secretion, resulting in a blunted, less diurnal pattern (Janssens *et al* 1995). The cortisol secretion pattern of sheep following 60 days of confinement is flatter than the cortisol profile earlier in the period of confinement (Fordham *et al* 1991). A disappearance of the normal rhythmicity of cortisol secretion is also seen in ewes given repeated electric shocks to a foreleg (Przekop *et al* 1985). Chronic stress increases the ability of the adrenal glands to secrete glucocorticoids, resulting in a potentiated response to acute stressors in chronically stressed animals (Jensen *et al* 1996; Terlouw *et al* 1997). The cortisol response to adrenocorticotrophic hormone (ACTH) administration is greater in confined sheep than in sheep maintained in paddocks (Bowers *et al* 1993). The HPA axis response to long-term stress in the sheep therefore involves changes in control systems such that basal plasma cortisol may return to, or fall below, pre-stress levels concomitant with an increased pituitary–adrenocortical response to additional psychological stressors.

Abnormal reactivity of heart rate and temperature changes are also features of the chronic stress response (Wiepkema & Koolhaas 1993), through activation of the SAM system. Chronic stress is not accompanied by changes in easily measurable variables in this system, such as plasma catecholamines or heart rate (Terlouw *et al* 1997). In pigs, Schrader and Ladewig (1999) demonstrated that neither heart rate nor adrenaline release were normalised on repeated separation from the social group, whereas parameters of the HPA axis declined with repetitions. However, there is evidence from pigs and rodents that chronic stress is associated with changes in catecholamine biosynthesis (Johnson *et al* 1992) and with changes in the control of cardiac function, particularly when additional stressors are applied (Schouten *et al* 1991). In sheep moved into isolation chambers, metabolic rate and heat production are elevated and do not show apparent normalisation until after 40 days of isolation (Adrichem & Vogt 1993). Likewise, social isolation elevates the heart rates of sheep above the levels exhibited prior to isolation (Cockram *et al* 1994), and this persists for the duration of a 9 h separation, although this was not seen after the sheep were separated for the seventh time. Wiepkema and Koolhaas (1993) conclude that abnormal reactivity of the neuroendocrine systems, especially heart rate and temperature changes, are a feature of the chronic stress response. In humans, primates and rodents, chronic stress may facilitate cardiovascular disease and hypertension, which may be related to alterations in the control of cardiac activity.

Other physiological responses to chronic stress in sheep

Reproduction

Social rearing conditions affect the interest shown by rams towards oestrous ewes (Zenchak & Anderson 1980). The incidence of barren ewes is increased by sub-optimal housing conditions (Bush & Lind 1973; Sabrh *et al* 1992) and, in young ewes, by psychological stressors prior to mating (Knight *et al* 1988). Oestrus behaviour is reduced at high stocking densities (Sabrh *et al* 1992), and transport, isolation or cortisol administration can block or delay oestrus (Ehnert & Moberg 1991). Restraint, confinement or transport suppress follicular growth and development by blocking or delaying the pre-ovulatory surge of luteinising hormone (LH) (Rasmussen & Malvern 1983; Dobson & Smith 1995; Dobson *et al* 1999). Stress also has effects at the level of the hypothalamus or higher brain areas, affecting gonadotrophin-releasing hormone (GnRH) release in rams and ewes (Matteri *et al* 1984; Dobson & Smith 2000), and at the level of the pituitary by decreasing the amount of LH secreted in response to GnRH challenge (Dobson & Smith 2000). Stress therefore acts at multiple reproductive pathways such that reduced fertility occurs with chronic stress. Chronic stress results in a decrease in the number of ewes lambing and the number of multiple births (Knight *et al* 1988), lower milk yield and nutrient content in milk from dairy ewes (Sevi *et al* 1999, 2001) and impaired maternal behaviour (Kiley-Worthington 1977). These effects may be particularly evident in younger animals (Knight *et al* 1988).

Growth, wool and meat quality

Sheep kept at higher stocking densities or in metabolism crates have reduced growth rates (Gonyou *et al* 1985; Abdel-Rahman *et al* 2000) compared to animals kept at lower stocking densities, or before isolation. Artificially reared lambs also have lower growth rates than do ewe-reared lambs (Napolitano *et al* 2002). These effects may be secondary to alterations in feed intake. Plasma cortisol levels and growth rate are poorly related in sheep (Purchas *et al* 1980), and infusing cortisol does not affect basal growth hormone (GH) release (Thompson *et al* 1995). However, the release of GH from the pituitary in response to exogenous growth-hormone releasing factor is attenuated in sheep given cortisol (Thompson *et al* 1995). Sheep given exogenous cortisol show reduced wool growth, reduced staple-strength and increased fibre-shedding (Ansari-Renani & Hynd 2001; Schlink *et al* 2002). Impaired wool growth is also a symptom of chronic lameness and parasitism, although whether these effects are seen in psychologically stressed animals is not known. Restraint in isolation or rough transport causes increases in muscle pH and reduced glucose and lactate concentrations, thereby increasing the likelihood of dark cutting meat (dark, dry meat with a reduced shelf life caused by high pH post-mortem [Apple *et al* 1995; Ruiz-de-la-Torre *et al* 2001]). There is therefore some evidence that chronic stress impairs growth rate, wool growth, feed conversion efficiency and meat quality; however this is inconclusive, particularly for animals highly selected for growth rate or wool production. For example, Marsden and Wood-Gush (1986b) reported high levels of stereotypy or abnormal behaviours in sheep without effects on growth rate.

Immune function and parasite resistance

In sheep, stressors such as restraint, isolation or the removal of lambs from ewes, cause an increase in neutrophils and a decrease in lymphocytes in the blood (Minton & Blecha 1990; Coppinger *et al* 1991; Cockram *et al* 1993, 1994; Degabriele & Fell 2001). Stressed sheep also show reduced lymphocyte blastogenic responses when challenged with specific mitogens (Minton *et al* 1992, 1995; Cockram *et al* 1994; Sevi *et al* 2001). Thus, chronically stressed sheep do not mount as efficient a response to pathogen challenges as do unstressed animals.

Stress associated with transport and housing causes sustained elevation of faecal egg counts compared to pastured sheep (Sotiraki *et al* 1999). Following experimental infection, artificially weaned lambs also have significantly higher faecal egg counts than do control lambs that remain with their dams (Watson 1991). Control lambs have earlier and stronger serum antibody responses than do artificially weaned lambs.

Behavioural responses to chronic stress in sheep

As with physiological responses to chronic stress, behavioural responses also show a temporal pattern of adaptation, although this may not necessarily be a decline to pre-stress levels. Sheep transferred singly to indoor pens from pasture go through a period of behavioural inhibition or withdrawal, with increased time spent lying for the first weeks of confinement (Done-Currie *et al* 1984; Fordham *et al* 1991). Newly confined sheep also show a lack of environmental awareness and are inattentive to activities occurring around them (Done-Currie *et al* 1984). Thereafter there is an increase in behavioural activity, although the behavioural patterns shown differ from those of pastured sheep, and may include stereotypical behaviours (Done-Currie *et al* 1984; Marsden & Wood-Gush 1986a; Fordham *et al* 1991). Newly confined sheep drink less and ruminate more than long-term confined sheep (Done-Currie *et al* 1984). This may reflect either acute stress responses in newly confined sheep, or chronic stress in long-term confined sheep, but demonstrates the temporal change in behaviours that occurs over a period of confinement. The following behaviours or patterns of behavioural change have been reported in sheep under conditions of chronic stress.

Changes in activity patterns

Isolated, stall-housed sheep and ewes housed indoors show greater inactivity than do grouped or pastured sheep (Tobler *et al* 1991; Casamassima *et al* 2001). However, increased activity is reported in sheep subjected to frequent environmental changes (Sevi *et al* 2001), housed in large groups (Kiley-Worthington 1977), and moved from pasture to feed lots (Fell *et al* 1991). Confined animals show alterations in the circadian rhythm of behaviour or activity (as mentioned above for plasma cortisol): the onset and decline in activity patterns are more abrupt in confined animals than in sheep at pasture (Tobler *et al* 1991). Individually housed sheep exhibit waves of activity interspersed with inactivity throughout the day (Done-Currie *et al* 1984; Fordham *et al* 1991), in comparison to pastured sheep with their more pronounced diurnal rhythms of activity (Tobler *et al* 1991).

Aggression

Aggressive behaviours are very infrequent in pastured sheep compared to housed sheep (Lynch *et al* 1989). However, increased aggression, for example butting and chasing episodes (Done-Currie *et al* 1984), is observed under a number of conditions, including sudden environmental and social change, lack of space, large social group size and when food or feeder space is restricted (Arnold & Maller 1974; Kiley-Worthington 1977; Done-Currie *et al* 1984; Sevi *et al* 2001).

Changes in feed and water intake

Sheep isolated, or housed in metabolism crates, have reduced water intakes (Parrott *et al* 1987), reduced feed intakes (Abdel-Rahman *et al* 2000) and disturbed feed intake patterns (Done-Currie *et al* 1984). Failure to eat has also been reported in sheep subjected to simulated sea voyages (Hodge *et al* 1991), and nearly 50% of deaths during actual voyages are attributed to inanition or reduced feed intake (Richards *et al* 1989). However, the deaths of about 7% of sheep during voyages are attributed to metabolic disorders associated with over-eating.

Abnormal behaviours

Stereotypic, or repetitive, functionless behaviours, are seen less frequently in ruminants, and in sheep in particular, than in other species (Houpt 1987; Lawrence & Rushen 1993). This may be because sheep are less frequently kept in the type of housing that appears to elicit stereotypy; although an alternative hypothesis is that rumination acts to alleviate some of the experience of the stress conditions in a similar way to stereotypies (Fraser & Broom 1990). Individually housed sheep have, however, been shown to demonstrate stereotypical oral behaviours, such as mouthing bars, chewing slats or chains, rattling or chewing buckets, biting and chewing pen fixtures, mandibulation (licking lips and mouthing air), and repetitive licking (Lynch & Alexander 1973; Done-Currie *et al* 1984; Marsden & Wood-Gush 1986a,b; Fordham *et al* 1991; Cooper *et al* 1994, 1995; Cooper & Jackson 1996; Yurtman *et al* 2002). Locomotor stereotypies have also been reported, including rearing against the pen, repetitive butting, star-gazing (arching the head and neck over the back), leaping vertically up and down, weaving and route-tracing (Done-Currie *et al* 1984; Marsden & Wood-Gush 1986a). These studies suggest that sheep do perform stereotypies, although they may not be as frequent as in other species.

Feed restriction, particularly of energy, or a diet largely of molasses, increases the frequency of abnormal oral behaviours (Done-Currie *et al* 1984; Marsden & Wood-Gush 1986a; Cooper *et al* 1994; Yurtman *et al* 2002). Providing hay or increased fibre in the diet reduces oral stereotypy (Done-Currie *et al* 1984; Cooper *et al* 1995), and increases lying and rumination (Cooper & Jackson 1996), although not in all studies (Yurtman *et al* 2002). These data partially support the contention above (Fraser & Broom 1990) that when animals are fed diets that allow rumination the frequency of stereotypy decreases, perhaps because ruminating buffers the sheep from the effects of chronic stress. However, a similar relationship between feed intake, feed bulk and stereotypy is also seen in non-ruminants (Terlouw *et al* 1991), suggesting that feed bulk may lead to an increase in time spent feeding and a decline in stereotypy in a manner unrelated to rumination.

Sheep also show other forms of abnormal oral behaviours, including wool-biting or pulling and re-directed sucking. Wool-pulling occurs exclusively within indoor, restrictive enclosures (although there may also be a component of dietary deficiency [Fraser & Broom 1990]), and disappears when the sheep are turned out. Wool-pulling is generally performed by the most dominant sheep and is directed at subordinates (Fraser & Broom 1990; Lynch *et al* 1992); it is most frequent at high stocking densities and can be eliminated by increasing space per animal (Fraser & Broom 1990). Re-directed sucking occurs in artificially reared lambs and involves sucking of the navels and scrotums of other lambs (Stephens & Baldwin 1971). This can persist until weaning, and seems to occur most frequently in lambs that have been disturbed during feeding. Lambs separated from their dams for 48 h in the first few days after birth, but subsequently raised by their dams, also show a propensity to perform re-directed sucking, even at 2 months of age (Markowitz *et al* 1998). Some lambs also chew and suck bedding, and stone sucking occurs in early weaned lambs (Jagusch *et al* 1977). Rumination begins as early as 2 weeks of age in artificially reared lambs (Stephens & Baldwin 1971), compared to approximately 4–5 weeks of age in dam-reared lambs (Dwyer *et al* 2001). This may reflect differences in nutrition, or that rumination is acting as a coping mechanism in chronically stressed sheep.

Isolation-reared lambs, when stressed, show a 'flank-touching' behaviour, characterised by the lamb reaching back and touching its own flank with its muzzle, which is not seen either in dam- or peer-reared lambs under the same conditions (Moberg & Wood 1982). Ewes frequently nuzzle their lambs' rumps, particularly when the lamb is sucking, and artificially reared lambs in groups also turn their bodies to touch rumps whilst sucking (Stephens & Baldwin 1971), suggesting that this may function as a comfort behaviour in lambs.

2. On-farm conditions and consequences for chronic stress

There are a number of specific management conditions that may cause chronic stress in sheep. Using the assessment tools identified in the earlier part of this review, the likelihood of chronic stress and poor welfare under various conditions will be considered.

Husbandry and stockpersonship

Aversion learning behavioural techniques demonstrate that sheep find isolation, capture and inversion more aversive than physical restraint with other sheep or human presence (Rushen 1996). Sheep are also known to find shearing stressful (Hargreaves & Hutson 1990; Rushen 1996; Mears *et al* 1999). Sheep have an excellent memory for place and good spatial learning abilities (Hutson 2000). They rapidly associate places with particular aversive experiences and can retain this information for up to a year (Hutson 1985), such that even the sounds of shearing are sufficient to elicit behavioural signs of aversion in previously shorn sheep (Mears *et al* 1999). Sheep are also able to discriminate between human handlers on the basis of their previous experience of pleasant or unpleasant treatment from the handler (Fell & Shutt 1989; Boivin *et al* 1997).

During handling, sheep are usually moved using fear-evoking stimuli (Gonyou 2000; Hutson 2000), and handling procedures are often aversive. Thus, distress in sheep is almost implicit in their handling. Sheep are often moved using dogs, often with other frightening stimuli, to elicit a flight response. As animals move towards the place of treatment (eg for shearing), particularly if they already associate that place with negative experiences (Rushen 1990, 1996), the effectiveness of fear stimuli in forcing movement declines as the animal's competing aversion to the place increases (Hutson 2000). Use of greater fear or force causes behaviours such as freezing, fleeing, baulking, sitting, turning, reversing and jumping or escape attempts. The amount of distress that sheep suffer during movement and handling is therefore likely to be affected by the quality of the stockperson working with the sheep (reviewed by Rushen & de Passillé 1992; Hemsworth & Coleman 1998; Hutson 2000). Thus, both the handler's behaviour, as well as that of the animals, is important to give an assessment of the stress associated with handling (Grandin 2000). The quality of sheep handling at market places and slaughterhouses can also be determined by the incidence of carcass bruising (Cockram & Lee 1991; Jarvis & Cockram 1994; Jarvis *et al* 1996). Most bruising appears to arise from wool pulls, hits and crushing of animals against pen structures, and from the riding of sheep when forced into confinement. Thus the incidence of bruises and injuries, the amount of noise and force applied to the sheep, the frequency of wool pulls, hits and riding incidences, and the incidences of baulking, turning and escape attempts may all indicate chronic stress associated with poor handling or poor stockpersonship.

Sheep that have been stroked and fed by a human over a number of days, approach humans more readily and have shorter flight distances and lower heart rates than do unhandled sheep (Hargreaves & Hutson 1990; Mateo *et al* 1991). In sheep, 'gentling' therefore seems to reduce fear of humans, and appears particularly effective when applied to young animals (eg Markowitz *et al* 1998). Early handling of lambs reduces their fear responses to subsequent isolation, restraint and capture (Uetake *et al* 2000). However, gentled sheep show similar struggling responses to restraint (Mateo *et al* 1991) and aversion to sham-shearing (Hargreaves & Hutson 1990) compared to sheep that have not been gentled. Thus, although gentling reduces fear, this may not generalise to other aversive procedures, but may ease handling of sheep when the procedures are not aversive.

Many sheep, particularly those kept under extensive conditions, are worked with dogs, usually for herding rather than for guarding (Coppinger & Coppinger 2000). However, the presence of a dog or recorded dog barking is used as a stressor in experimental studies and causes elevations in plasma cortisol, ACTH, heart rate and body temperature above those observed upon exposure to humans and noise (Harlow *et al* 1987; Baldock & Sibley 1990; Cook 1996; Komesaroff *et al* 1998). Thus, in the same way that the behaviour of the stockperson is likely to influence the levels of stress experienced by sheep during routine handling, the behaviour of sheepdogs is also a potential source of chronic stress.

Competition

Sheep have a preferred distance to maintain from other flockmates or a 'personal space' (Lynch & Alexander 1973). This varies between breeds, with some breeds have greater tolerance for the presence of other sheep. However, agonistic encounters and a social hierarchy appear when sheep are crowded together and resources are limited (McBride *et al* 1967). Many expressions of dominance in sheep are not necessarily associated with overtly aggressive behaviours. Sheep maintain social hierarchy through more subtle behaviours associated with head movement and eye contact. Dominant sheep displace subordinates from feed troughs and preferred lying positions by resting their chins on the backs of the subordinates or by pawing (Done-Currie *et al* 1984). When feeder space is limited, the number of displacements or disturbances from the trough increases (Arnold & Maller 1974), and a progressively greater proportion of sheep cease to compete for food. Subordinate sheep may also be displaced from shelter or shade during conditions of thermal extremes if space is limited (Sherwin & Johnson 1987; Deag 1996). Subordinate animals are therefore likely to have a lower feed intake; they are usually at the tail of movement order and are likely to eat the poorer quality or contaminated forage leading to higher worm burdens (Lynch & Alexander 1973). Subordinates also have greater behavioural and plasma cortisol responses to additional acute stressors (Kilgour & de Langen 1970), and are more likely to be victims of wool-pulling (Lynch *et al* 1992).

In groups of rams, subordinate animals mate less preferred ewes, and mate fewer ewes when more rams are present (Tilbrook *et al* 1987). Although there is no difference in conception and lambing rates between dominant and subordinate Bighorn sheep (Hass 1991), dominant animals spend more time suckling their lambs than do subordinates (which may reflect better nutrition), and are more likely to adopt alien lambs. The behavioural and physiological evidence therefore suggests that even in the absence of overt aggression, subordinate sheep may be chronically stressed, particularly when resources are limited and competition is high.

Weaning stress

Natural weaning is a gradual process whereby the bonds between ewes and lambs gradually decline. Associations between ewes and lambs remain strong up to 100 days after birth (Arnold *et al* 1979), and, even though they no longer suck from them, lambs maintain spatial contact with their dams up to 190 days after birth (Arnold & Pahl 1974). Artificial weaning is abrupt, and lambs are usually separated before they are nutritionally weaned from their mothers and always before they are psychologically weaned. They may also be exposed to other potentially stressful events such as regrouping or mixing, transport and/or removal to a new environment. Abrupt weaning at 3–4 months of age causes a transient increase in plasma cortisol in lambs (Mears & Brown 1997; Rhind *et al* 1998; Orgeur *et al* 1999), which is not attributable to nutritional factors (Rhind *et al* 1998). Elevations in cortisol are greater if the separation is total compared to if ewes and lambs are able to see one another (Orgeur *et al* 1999). Behaviourally, abrupt weaning is associated with increased behavioural activity, increased vocalisation, disruption of circadian rhythms of activity, decreased social distance and the formation of larger social groups (Veissier *et al* 1989; Pollard *et al* 1992; Orgeur *et al* 1998, 1999; Dwyer & Lawrence 2000). Abrupt weaning is also associated with depressed growth rates (Jagusch *et al* 1977; Watson 1991; Napolitano *et al* 1995) and increased susceptibility to disease (Jagusch *et al* 1977; Watson 1991).

Lameness

Lameness in sheep is very common and is under-emphasised as a cause of suffering and distress. 85% of lameness in sheep is caused by foot rot (infection with *Dichelobacter nodosus*), which is endemic in the UK (more than 90% of farms report at least one case per year; on average 6–11% of sheep are affected annually [Royal Veterinary College survey 1997]). The clinical symptoms are varying degrees of lameness (from transient and mild to persistent and severe), recumbency and reluctance to move, reduced feed intake, low body weight and reduced wool growth (Marshall *et al* 1991; Egerton 2000).

Experimentally, sheep with severe foot rot have low plasma cortisol and a tendency towards elevated vasopressin and prolactin (Ley *et al* 1991a); although similar experiments carried out in field trials reported elevated plasma cortisol when lesions were severe (Ley *et al* 1994). These differences may reflect differences in the time course of the apparent normalisation of HPA reactivity to chronic stress (Jensen *et al* 1996) or a greater acute response to handling in experimentally naïve sheep suffering from chronic stress. Sheep with mild or severe foot rot show elevated plasma adrenaline and noradrenaline levels (Ley *et al* 1992). Severe foot rot is also associated with a significantly reduced threshold for nociceptive stimuli compared to healthy controls, indicating an increased sensitivity to acute pain (Ley *et al* 1989, 1995). The analgesic effectiveness of xylazine is also reduced with chronic foot rot (Ley *et al* 1991b). Treatment of foot rot and the apparent resolution of its clinical symptoms is not accompanied by an alteration in nociceptive threshold for at least 3 months. Thus, although the sheep are not judged to be lame, they are still more sensitive to acutely painful stimuli.

Endoparasitism

Gastrointestinal helminth infections cause acute and chronic disease but, with the use of antihelminthics, varying degrees of subclincial infections, in which sheep may appear healthy, are more common (Coop & Jackson 2000). Animals with sub-clinical parasitic infection show reduced feed intake and utilise nutrients less efficiently than do non-parasitised animals (Coop 1979). Parasitised sheep also have reduced growth rates, reduced wool production, increased mortality (especially in young sheep), reduced milk production and reproductive success, and are more susceptible to fly strike (Coop 1982; Anderson *et al* 1987; Waller *et al* 1987a,b; Festa-Bianchet 1988). The growth effects may be secondary to a reduction in feed intake. Sheep infected with *Haemonchus* or *Trichostrongylus* have elevated plasma cortisol (Prichard *et al* 1974; Fleming 1997) and low thyroxine (Prichard *et al* 1974). These effects cannot, however, be entirely attributed to reduced feed intake since pair-fed sheep do not show the same decrease in thyroxine, and cortisol elevation is less marked (Prichard *et al* 1974).

Although all sheep tend to avoid areas of the sward contaminated with faeces, sub-clinically parasitised animals are more selective than uninfected animals (Hutchings *et al* 1998) and reject even high quality swards if contaminated (Hutchings *et al* 1999). They also spend less time grazing, are less active than uninfected sheep and have reduced herbage intakes (Hutchings *et al* 2000). Lambs born to Bighorn ewes with high worm burdens have shorter suckling bouts and reduced survival compared to those born to ewes with low worm burdens (Festa-Bianchet 1988), suggesting that sub-clinical infections have nutritional and reproductive consequences.

Ectoparasitism

Sheep are susceptible to a number of bacterial and parasitic diseases involving infestation of the fleece, including sheep scab, or *Psoroptic* mange — an acute or chronic form of allergic dermatitis (Bates 2000). Early infestations may take some days before symptoms are manifest as the host sheep becomes increasingly sensitised to the mites. At this stage of the disease, sheep may show disturbed behaviour patterns: restlessness, disturbed lying behaviours, intense rubbing of areas of the fleece, biting at the flanks and head tossing (Sargison 1995; Bates 1997; Corke & Broom 1999; Berriatua *et al* 2001). Rubbing behaviours are related to the development of the scab lesions (Bates 1997; Berriatua *et al* 2001). As the disease progresses, infected sheep become increasingly distressed and agitated by the presence of the allergens. They show increased rubbing and head tossing, and stereotypic nibbling or mouthing responses (in the absence of stimuli) characterised by lip-smacking and tongue protrusion (Sargison 1995; Corke & Broom 1999). Sheep can also become infested with *Psoroptes* species mites within the ear canal (Bates 2000), even in the absence of sheep scab infection (Bates 1991b). Behaviourally, affected sheep exhibit head tossing or shaking, ear rubbing and scratching (Bates 1991b, 1996). Clearly, sheep scab causes intense distress to sheep. Since allergic symptoms are related to the formation of lesions (Bates 1997), and may persist for the duration of the lesion, even after treatment has killed the mites (Bates 1991a), techniques for the early detection and treatment of the infestation are essential to prevent excessive suffering.

Fly strike, or cutaneous myiasis, is a major disease problem of sheep farming, and may frequently go unnoticed in extensive farming conditions (Bates 2000). Fly strike is most common in lowland farms, particularly in warm and wet areas, and where sheep are kept at high stocking densities (French *et al* 1994). Fly strike causes depression in feed intake, growth rate and wool growth (Heath *et al* 1987; Walkden-Brown *et al* 1999a), accompanied by elevated body temperature, plasma ACTH and cortisol, and decreased plasma glucose and β-endorphin (Shutt *et al* 1988; Walkden-Brown *et al* 1999b). Initially, infestations are accompanied by behavioural indicators of distress, including agitation and dejection (Bates 2000). Stamping, vigorous shaking of the tail, and gnawing or rubbing at the infested areas develop as the infestation continues. Fly strike occurs in waves and untreated animals may suffer primary, secondary and tertiary attacks before death.

Thermal stressors

Ruminants have a marked ability to alter their zone of thermal neutrality in response to previous thermal history (Webster 1983), thus sheep are able to adapt physiologically and behaviourally to regulate heat loss and to cope with thermal extremes. With shade, sheep are able to maintain body temperature in ambient temperatures of up to 50°C

(Johnson 1987). In hot weather, diurnal activity patterns are also adjusted to the coolest parts of the day (Silanikove 2000). Lambs and lactating ewes in particular make use of shelter when temperatures are low, wind speed is high and when it is raining (Lynch & Alexander 1976; Alexander *et al* 1979; Pollard *et al* 1999). Thus, behavioural mechanisms appear to be important for dealing with thermal extremes in sheep. Traditional hill sheep farming practices that allow for the formation of home ranges, within which ewes of the same social group restrict themselves to particular areas and become familiar with the location of resources such as food, water and shelter (Hunter & Milner 1963; Hewson & Wilson 1979; Lawrence & Wood-Gush 1988), facilitate these behaviours. Sheep may, however, experience distress under thermal extremes if confined within open and exposed pastures lacking in shelter.

Nutritional stressors

Sheep may undergo prolonged periods of under-nutrition, particularly extensively farmed sheep during the winter period (eg Waterhouse 1996). Sheep graze for about 8 h each day, but can increase this to 13 h when food is limited (Lynch *et al* 1992). An important constraint on the time budget of ruminants is the need to find time to ruminate (Low *et al* 1981), thus sheep cannot increase intake maximally to compensate for low food availability or poor quality. Deprivation of food for 6 h causes an increase in feeding motivation in sheep (Jackson *et al* 1999a) that is greater than their desire for water after 24 h deprivation (Jackson *et al* 1999b). After 24 h food and water deprivation, sheep show increased plasma free fatty acids and β-hydroxybutyrate, but no biochemical indication of dehydration (Cockram *et al* 1997). These data suggest that sheep have increased feeding motivation after periods without food, and this appears to be greater than their motivation to drink; however, whether this is associated with hunger and distress is unclear. For example, sheep undergo seasonal reductions in voluntary feed intake and metabolic rate (Argo & Smith 1983; Argo *et al* 1999) that may reflect adaptation to the seasonal cycle of feed availability. Lamb survival, however, is greatly affected by the nutritional intake of the ewe during pregnancy (reviewed by Waterhouse 1996), and the relationship between the ewe and lamb is affected by even moderate under-nutrition (Dwyer *et al* 2003). This can lead to starvation, hypothermia and consequent suffering in the lamb. Thus, although it is not clear whether sheep experience hunger and distress when food is scarce, under-nutrition is associated with other welfare issues, such as increased lamb mortality.

Conclusions

Although chronic stress responses can be difficult to interpret, there are a number of conditions in which an extensively husbanded animal — the sheep — appears to suffer chronic stress. Animals can have apparently normal cortisol or heart rate responses, but continue to show extremely abnormal or disturbed behaviours because systems adapt in order to maintain sensitivity to further acute pain or stress. Chronically stressed sheep, for example subordinate animals or animals experiencing chronic lameness, also show hyper-responsiveness to further acutely stressful stimuli. Behavioural indicators of chronic stress mainly comprise changes in ongoing behaviour patterns: increased apathy or low levels of activity under some conditions, particularly those of behavioural restriction or confinement; hyperactivity, agitation or aggression with rough or pressured handling, high stocking density or confinement and some disease conditions such as ectoparasitism; and decreased feed intake with some disease conditions, including lameness, internal and external parasitism and other conditions of chronic stress such as isolation, restraint or high stocking density. However, these measures may not be easily observed in on-farm situations without prolonged inspection. Circadian rhythms of behaviour are altered when an animal is distressed by, for example, weaning (Veissier *et al* 1998) or confinement (Tobler *et al* 1991). Since unstressed sheep show pronounced circadian rhythms in feeding, rumination, camping and movement, deviation from group activities may identify chronically stressed sheep.

In other species, abnormal or stereotypic behaviours are commonly associated with animals having experienced chronic distress. In sheep, stereotypic behaviours, for example abnormal oral behaviours, are less frequently observed, and usually seen only under highly artificial conditions when sheep are housed individually. However, other behaviours (eg re-directed sucking, wool pulling) may be more frequent when rearing or housing conditions are sub-optimal. Whether or not rumination functions as an alternative coping strategy in sheep, and the role of rumination in reducing chronic stress responses, requires further investigation.

Other indicators of chronic stress rely on the effects of stress on other systems: reduced immunity and a higher incidence of disease or worm burdens, impaired reproduction and reduced body and wool growth. Although these have the advantage of being easy to interpret, they are the consequences of an animal suffering distress rather than a direct indication of that distress. Furthermore, in animals selected for reproduction or growth and fed high quality feeds, these indicators may be relatively insensitive. The behaviour of stockworkers and sheepdogs may also induce chronic distress. Thus, assessment of the behaviour and handling skills of stockworkers may also be used in the assessment of animals experiencing chronic stress and as indicators of poor welfare.

Animal welfare implications

The responses of sheep to chronic stress are diffuse and subtle. Since stereotypy is infrequently expressed in sheep, the main behavioural responses are alterations in patterns of behaviour, such as feeding or activity, and in circadian rhythms. Evidence of neuroendocrinological and physiological alterations as a result of chronic stress can be seen in impaired reproduction, reduced growth, wool and meat quality, impaired disease resistance and increased parasite burdens. The evidence presented suggests that a number of management conditions, including aspects of handling by stockworkers and sheepdogs, limited resources leading to competition, and weaning, lameness and parasitism, are potential sources of chronic stress and poor welfare in sheep. Whether thermal conditions or low feed availability are also sources of chronic stress is less clear, particularly if sheep are given the opportunity to show behavioural adaptations (such as shelter seeking). Under-nutrition may still cause poor welfare in sheep, although this may have its main impact on lamb survival rather than through chronic stress of the under-nourished ewe. However, the existence of many sources of chronic stress in the management of sheep suggests that the welfare of this species requires more attention than it has currently received.

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