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The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK

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Selection for easier managed sheep

J Conington*, J Collins and C Dwyer

Sustainable Livestock Systems, Scottish Agricultural College, West Mains Road, Edinburgh EH9 3JG, UK
* Contact for correspondence and requests for reprints: Jo.Conington@sac.ac.uk

Abstract

Current alterations in the farm environment, such as a reduced number of farm workers, may mean that sheep genotypes that are highly dependent on man for nutritional and reproductive success will experience poorer welfare within that environment. In the past 30 years, average flock size has doubled, and flocks of over 1,000 ewes managed by one stockperson are common. The reduction in the ratio of stockpeople to sheep affects animal welfare, with less time for tasks such as healthcare and inspection. It has also led to increased interest in the development of new genotypes that are better able to look after themselves. Selection and management of sheep to promote behaviours associated with survival, and selection of robust animals that require less human intervention for good welfare, are important breeding goals. As these animals will receive less inspection at close quarters, selection for resistance to disease will have significant animal welfare benefits. In addition, the development of sheep lines that require little or no intervention at lambing will be important. In areas where wool is not valuable, the use of wool-shedding breeds to avoid the stress associated with shearing, and to reduce the incidence of flystrike are already proving to be beneficial. Importantly, this selection should not be interpreted as providing no care to these animals, and careful management during the production of these genotypes is needed to avoid at least transient welfare problems where genotypes and environment (eg lower shepherding) are mismatched.

Keywords: *animal welfare, behaviour, breeding, disease resistance, low input, sheep*

Introduction

The trend in Europe towards more extensive rearing conditions in areas of intensive production and towards the maintenance of farming activity in less favourable regions, will lead to considerable changes in sheep management. Greater emphasis will be placed on the adaptation of animals to their environment and on their behavioural response to different stressors. Better handling and management practices enable greater numbers of sheep to be looked after per labour unit and it is now common practice for a single shepherd to be responsible for more than 1,000 sheep. Less time for specific tasks may lead to reduced input in areas such as supplementary feeding, healthcare, and inspection of stock. Reduced levels of supervision may mean that disease, injury and parasitism, for example, go undetected and untreated. Furthermore, modern farmed breeds, bred and raised under intensive conditions, may not be adequately adapted for more extensively managed systems and may not be able to survive and thrive in situations where there are fewer human inputs. Animal welfare could consequently be compromised due to insufficient animal care.

It is widely recognised that some breeds are easier to look after than others. For example, Blackface ewes require less intervention at lambing compared to Suffolks, and lambs take a shorter time to stand and suck after birth (Dwyer & Lawrence 2005). However, many farmers are reluctant to substitute their existing breeds for easier managed ones entirely, to prevent the loss of other important characteristics, such as carcase conformation and growth. For this reason, new breeding tools are required to facilitate within-breed selection for traits that confer greater efficiency and easier management, whilst retaining the desired growth and other performance characteristics.

The purpose of this paper is to investigate the potential for selecting for traits to improve sheep welfare in systems with reduced human intervention. The traits that confer better adaptation to low input systems are considered to be: i) resistance to disease; ii) behavioural, particularly those associated with survival; and iii) physical, such as the ability to shed wool. Improvement in some of these traits may involve a reduction in productivity, however there is evidence that sheep strains can be developed that have improved functional traits, whilst still retaining production characteristics. For example, the 'Marshall easy care' Romney from New Zealand, is a strain with a reputedly high survival rate, minimum birthing problems, excellent growth rate, good mobility, good wool production (4–6 kg per annum) and the ability to thrive in harsh conditions. Likewise, the 'Easycare' breed (derived from Welsh Mountain, Cheviot and Wiltshire Horn breeds) requires

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minimal shepherding and veterinary care and yet offers good meat yields and lambing ratios. This breed also sheds its wool, which reduces sheep stress and labour costs associated with shearing (Vipond 2006). The likely welfare benefits and the potential for improvement in selected traits will now be considered.

Breeding for resistance to disease

Disease affects animal welfare and also influences production economics and food safety. Prevention of diseases will usually be preferable to curing them, particularly from an animal welfare viewpoint, and in cases where there is genetic variation in resistance to a disease, selection may be a useful preventative measure. This approach may be particularly useful in extensive systems where the animals cannot be inspected as regularly as those kept more intensively. Some examples of the potential to select for disease resistance will be considered here.

Nematodes

Gastrointestinal nematode infection is possibly the most significant disease challenge facing ruminants (Perry & Randolph 1999). The clinical symptoms of infections are diarrhoea, dehydration, loss of appetite, failure to gain weight and anaemia in *Haemonchus* infections. Sheep that are outwardly healthy but have subclinical parasitism still display symptoms that suggest their welfare may be compromised. These include a reduction in their voluntary feed intake, reduced growth rate, reduced wool production, increased mortality (especially in young sheep), reduced milk production, reduced reproductive success, and an increase in the frequency of succumbing to flystrike (Coop 1982; Anderson *et al* 1987; Waller *et al* 1987a,b; Festa-Bianchet 1988).

Between- and within-breed genetic variation in resistance to nematodes has been demonstrated extensively (eg Bishop *et al* 1996; Woolaston & Piper 1996; Morris *et al* 1997, 2000a; Stear *et al* 1997; Smith *et al* 1999; Woolaston & Windon 2001). Genetic differences between host animals in nematode parasite resistance have also been observed for a variety of parasite species. There are a number of methods for quantifying resistance, including faecal egg count (FEC: the number of eggs per gram of faeces), phenotypic physiological markers (such as plasma immunoglobulin A activity; Strain *et al* 2002), or host immunological response by saliva swab. Of these, FEC has been most studied, and heritability estimates lie between 0.2 and 0.4 (reviewed in Safari & Fogarty 2003; Pollot & Greef 2004), ie moderately high and similar to most performance traits in lambs. Resistance to different species of nematodes tends to be related, with genetic correlations between the FEC values arising from different genera of parasites generally being close to 0.5 (eg Bishop *et al* 2004). This means that in practice, it might not be necessary for the presence of all genera to benefit from selection strategies to improve host genetic resistance. Selective breeding using FEC as an indicator trait for nematode resistance has been shown to be effective (Woolaston & Piper 1996; Morris *et al* 1997, 2000a; Woolaston & Windon 2001) and is thus a method that could improve sheep welfare in lower input systems. Added benefit is also obtained from genetically reducing FEC and, hence, pasture contamination, as sheep grazing this pasture face a lower level of challenge (Gruner *et al* 2002; Leathwick *et al* 2002). In these studies, the grazing of fields by 'susceptible' sheep led to considerably heavier pasture contamination, increased FEC and reduced performance, than grazing by 'resistant' sheep.

Faecal contamination of wool and blowfly strike

Accumulated faecal matter in the wool of the breech area (referred to as 'dags'), has been investigated as a possible indirect indicator trait to breed for decreased worm-related diarrhoea or scouring (Greeff & Karlsson 1997; McEwan *et al* 1997). The presence of soiled fleece also increases the likelihood of blowfly strike (French *et al* 1995). Blowfly strike is caused by the invasion of living tissue by the larvae of dipteran flies, primarily the sheep blowfly (*Lucilia sericata*) (MacLeod 1992; Morris & Titchener 1997). The maggots feed directly on the infested sheep, creating serious welfare problems: affected animals are restless, dull and reluctant to graze, and kick at the struck area. Secondary bacterial infection often occurs and the animal may die of septicaemia or the absorption of toxins from liquefied body proteins. Clipped sheep and young lambs with short fleeces are not usually attacked, but as the length of the fleece increases, so does the risk of strike (French *et al* 1996).

Dag Score (DS: assessment of faecal soiling) seems to be a moderately heritable trait (between 0.25 and 0.35; reviewed in Pollot *et al* 2004). However, many studies have found DS to be unfavourably correlated with FEC, suggesting that selection for decreased FEC will result in an increase in DS (Watson *et al* 1986; Baker *et al* 1991; Pollot *et al* 2004). Thus, despite this trait generally being used as an indicator of host resistance to parasites, the poor relationship with FEC implies that it would be ineffective in terms of improving host resistance to parasites. However, selection for DS in its own right could be important to decrease the occurrence of scouring in sheep (Pollot *et al* 2004) and to reduce the incidence of blowfly strike. If both FEC and DS are combined into a selection index, then it is likely that improvements in host resistance and reduced scouring could be achieved simultaneously.

Differences exist both between and within breeds in susceptibility to flystrike, with Merino sheep experiencing higher strike rates than other breeds (Litherland *et al* 1992; Rathie 1994). Large differences between Merino flocks in their susceptibility to flystrike are also reported (Dunlop & Hayman 1958; Atkins & McGuirk 1979; Raadsma *et al* 1989). Heritability estimates for prevalence of flystrike range from 0.10 to 0.58 (Atkins & McGuirk 1979; Gilmour & Raadsma 1986; Raadsma 1991). These data suggest that predisposition of sheep to flystrike is, in part, genetically determined, with potential scope for within-flock genetic improvement, at least within the Merino breed. The potential to select for Merino sheep with a bare breech area, and hence

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to reduce flystrike and the need for mulesing of sheep in Australia and New Zealand, has shown a moderate heritability for a bare breech (0.38–0.53; Edwards *et al* 2009). An alternative approach, for sheep breeds where wool is not valuable, is to introduce new genetic material into the population in an endeavour to make sheep less susceptible to blowfly strike, for example by the introgression of genes from the Wiltshire Horn breed in which fleece wool is shed annually (Slee & Carter 1961, 1962; Ryder 1969).

Footrot and other hoof disorders

Footrot, the major cause of lameness in sheep (Grogono-Thomas & Johnston 1997), is a significant welfare issue for the sheep industry. Footrot-affected sheep frequently experience pain, discomfort and lameness that affects their ability to compete for feed (Abbot & Lewis 2005). The clinical symptoms are varying degrees of lameness (from transient to severe), recumbency and reluctance to move, reduced feed intake, low bodyweight and reduced wool growth. With virulent (under-run) footrot, the clinical signs are more severe resulting in angry, red and swollen feet, complete detachment of the horn and spread of the infection to above the hoof (Winter 2004). Lame sheep are also more susceptible to other diseases because of their weakened condition. Selection to improve resistance to footrot would thus contribute significantly to improving animal welfare, particularly in systems with reduced inspection, as well as improving animal productivity.

Breed differences in susceptibility to footrot have been demonstrated by exposing animals to experimental or natural infection (Skerman *et al* 1982; Emery *et al* 1984; Stewart *et al* 1985; Cumlivski 1988; Lewis *et al* 1988), and by using hoof lesion scoring (Conington *et al* 2008a). There are also strong indications that within breeds, contradisposition to footrot infection is responsive to selection. For example, the heritability of hoof lesions ranges from 0.12 to 0.36 depending on the breed and prevalence level of footrot (Alwan 1983; Baker *et al* 1986; Raadsma *et al* 1994; Nieuwhof *et al* 2008; Conington *et al* 2010b). Although selection using footrot lesion scoring has been shown to be successful, because of the practical difficulties involved in objectively and repeatably scoring and classifying foot lesions, the use of a molecular genetic test for footrot resistance potentially brings enormous advantages. Furthermore, with genetic tests, animals that are candidates for selection do not have to be exposed to infection to determine genetic susceptibility. A test based on genetic polymorphisms within the MHC Class II region and response to footrot infection has been developed and used in New Zealand (Hickford *et al* 2000, 2004). The data suggest that selection to reduce footrot is possible and will therefore improve sheep welfare. As with selection for resistance to gastrointestinal parasites, a reduction in animals with footrot will lead to a reduction in the level of environmental contamination with footrot-causing bacteria (Nieuwhof *et al* 2009). Other causes of lameness such as white line degeneration ('shelly hoof') has largely been under-reported for sheep, although a recent UK study has shown it to be under moderate genetic control, and in some hill breeds, it has higher prevalence than classical footrot (Conington *et al* 2010a).

Mastitis

Mastitis is considered to be one of the most important health and welfare problems in dairy cattle and sheep (Leitner *et al* 2004; Heringstad *et al* 2005). It is also an important disease for some meat sheep breeds and is associated with pain in the ewe and impaired ewe-lamb interactions. There is almost no reported genetic data on mastitis in meat sheep, although in a review of breeding for resistance to mastitis, Conington *et al* (2008b) report that the estimates of heritability for Somatic Cell Count (SCC used as a proxy trait for mastitis) is low, ranging from 0.04 to 0.15. Despite this, selection for resistance to mastitis in sheep is currently underway in the French dairy sheep breed, Lacaune, (Rupp *et al* 2002) and in the Latxa breed in Spain (Legarra & Ugarte 2005). As it is estimated that mastitis costs approximately £11 per ewe in the UK for the Texel breed alone (Conington *et al* 2008b), selection for more resistant sheep for mastitis would go some way to improving the health and welfare of the UK sheep population.

Behaviour and lamb mortality

Lamb mortality is a significant welfare issue and a major constraint to efficient sheep production (Alexander 1988; Haughey 1991). The number of lambs weaned per breeding ewe has a greater influence on the productivity and profitability of most sheep enterprises than any other trait (Matos *et al* 1992). In addition, our recent research has shown a positive correlation between farm welfare scores and weaning percentage (Dwyer, unpublished report). Prolificacy or selection for higher litter size, despite the number of lambs born being positively correlated to the number of lambs reared, is also positively correlated to higher rates of mortality (Safari *et al* 2005; Sawalha *et al* 2007). Mortality amongst multiples is usually higher than amongst single-born lambs because of an increased risk of poor lamb behaviour and maternal desertion (Dwyer & Lawrence 2005) and lower bodyweight (Smith 1977; Hinch *et al* 1983; Elving *et al* 1986; Gama *et al* 1991; Fogarty *et al* 2000; Sawalha *et al* 2007). Breeding for higher litter sizes is thus not conducive to good lamb welfare. Selecting ewes that have the ability to successfully rear the lambs they gave birth to until weaning age is better for welfare, has a higher economic value than breeding for higher litter size *per se*, and is the preferred trait for selection (Conington *et al* 2004).

The vast majority of lamb deaths occur within 1–3 days of birth (Nowak *et al* 2000; Southey *et al* 2004). The first critical stage is the birth process itself, dystocia representing one of the major causes of mortality (Kerslake *et al* 2005). After birth, survival of the newborn will depend largely upon the quality of the interactions with the mother and her ability to provide the neonate with nutrition and protection (Haughey 1993), as well as the ability of the newborn to cope with the transition to neonatal life. Lamb mortality could therefore be reduced substantially by a shorter period of labour, by maternal behaviours that protect the nutritional and thermal state of

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the lambs and by lamb behavioural and physiological competency (Alexander 1988; O'Connor & Lawrence 1992; Dwyer & Lawrence 2005). This is particularly important in more extensive management systems where ewes must be able to conceive, carry, give birth to and rear their young with relatively little human intervention.

Lamb survival to weaning has a low heritability (0.02–0.13) suggesting that the scope for genetic selection to improve this trait is limited (Hall *et al* 1995; Lopez-Villalobos & Garrick 1999; Morris *et al* 2000b; Fadilli & Leroy 2001; Cloete *et al* 2002). However, Purser and Young (1983) reported that lamb-rearing ability was a repeatable trait, and that the more lambs reared, the better the subsequent performance appeared to be. Environmental variances due to permanent maternal effects (for example uterine capacity, pelvic width, milking and maternal ability) contribute most to the repeatability of ewe lamb-rearing performance (Morris *et al* 2000b), providing evidence that lamb survival is a result of a successful partnership between mother and offspring through pregnancy, parturition and lactation (Everett-Hincks *et al* 2005).

Various authors (eg Alexander *et al* 1990b; Cloete & Scholtz 1998; Kuchel & Lindsay 1999; Dwyer & Lawrence 2005; Dwyer 2008) have reported breed and line differences in lamb survival traits (eg length of parturition/ease of birth and neonatal progress of lambs). Conington *et al* (2001, 2006) predict that using multi-trait selection indices, improvements in maternal characteristics can be achieved alongside increasing lamb weaning and carcase weights, with little change in subjective lamb carcase quality traits. More recently, Sawalha *et al* (2007) estimated heritabilities for postnatal survival as being between 0.18 and 0.33 and suggested that both animal and maternal genetic effects should be included in breeding programmes for improving viability at birth. There are several candidate behaviours and traits, of both ewe and lamb, which would confer a survival advantage on the new-born lamb. Identification of these adaptations is an important first step if breeds that currently appear unsuitable for less-intensive systems are ever to be managed more extensively (Dwyer & Lawrence 2005). Some of these potential adaptations will be reviewed here.

Maternal care of the newborn

The formation of a close and exclusive attachment between the ewe and her lambs ensures early sucking and colostrum intake (Nowak *et al* 2000). Specific behaviours of the ewe (licking and grooming, low-pitched bleating, absence of aggression and lamb desertion, co-operation with lamb sucking behaviours) promote ewe-lamb attachment and mutual recognition (Alexander 1988; Nowak *et al* 1997, 2000; Dwyer 2008). The ewe forms an olfactory memory for her own lambs that allows her to restrict maternal care exclusively to her own offspring ('selectivity') (Poindron *et al* 1984a; Lévy *et al* 1995). As ewes are selective for their offspring, a lamb that fails to form an attachment with its dam will not be cared for by any other ewe and will not survive. The behaviours that promote selectivity include grooming and ewe-lamb contact (Baldwin & Shillito 1974; Poindron *et al* 1980; Alexander *et al* 1986; Poindron *et al* 1988; Lévy *et al* 1991; Hernandez *et al* 2001). Thus, ewe behaviour around lambing time has a large effect on lamb survival, particularly in extensive situations (Nowak 1996) and may also affect weaning weight of lambs and thus ewe productivity (O'Connor *et al* 1985; Lambe *et al* 2001).

Breed differences in the expression of maternal care have been demonstrated in several studies (Poindron *et al* 1984b; Dwyer *et al* 1998; Le Neindre *et al* 1998; Dwyer & Lawrence 1998, 1999, 2000) In studies of British breeds, Blackface ewes show more grooming behaviour and make more low-pitched bleats than Suffolk ewes, develop maternal selectivity more rapidly than Suffolk ewes, and are quicker to approach and spend more time with their own lambs in choice tests (Pickup & Dwyer 2002). Breed differences persist throughout lactation in ewes reared under identical conditions, and sire effects on maternal behaviour can be seen in cross-bred ewes (Pickup 2003). There are, however, no reported heritabilities for these maternal behaviours.

Maternal behaviour score (MBS)

The MBS is a scoring system developed by O'Connor *et al* (1985), based on the proximity of the ewe to her lamb as it is handled. It is related to both postnatal lamb survival and weaning weight (O'Connor *et al* 1985; O'Connor 1996; Lambe *et al* 2001; Everett-Hinks *et al* 2005; Sawalha *et al* 2007), and varies with ewe genotype (O'Connor *et al* 1985; Alexander *et al* 1990b). MBS increases with parity (Lambe *et al* 2001) indicating that maternal experience of the ewe is an important factor. This is in agreement with the known improvement in maternal care with maternal experience in sheep (O'Connor & Lawrence 1992; Cloete *et al* 1998; Dwyer & Lawrence 2000).

Estimates of heritability for MBS are consistently low (0.13, Lambe *et al* 2001; 0.09, Everett-Hincks *et al* 2005), but show a moderate positive genetic correlation with early lamb growth rate (Lambe *et al* 2001). However, MBS is not just a measure of maternal attachment but is also a measure of ewe temperament and reactivity to the presence of humans (Dwyer & Lawrence 2005; Sawalha *et al* 2007). The composite nature of this trait may partly explain the low heritability. However, for breeds with typically poor levels of maternal behaviour the inclusion of an MBS could be beneficial for easier managed sheep systems.

Neonatal lamb behaviour

Neonate survival is dependent on the co-ordinated expression of appropriate behaviours from both mother and young to ensure that the young is adequately fed and nurtured. In sheep, the role of neonate behaviour in ensuring survival becomes increasingly important and may be at least as important as that of the mother (Nowak *et al* 1997; Dwyer & Lawrence 1999). Lambs are born with limited tissue reserves so must suck soon after birth to survive. To suck successfully, the lamb must be able to stand and show appropriate udder-seeking behaviour and several studies have shown lamb survival is enhanced in lambs that stand and suck quickly after birth (Alexander 1958; Owens *et al* 1985; Cloete 1993; Dwyer *et al* 2001).

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The time taken by lambs to stand and to suck has been examined in several breeds and exhibits some genetic variation (Slee & Springbett 1986; Alexander *et al* 1990b; Cloete *et al* 1998; Dwyer 2003; Dwyer *et al* 2005). Cloete *et al* (2002) estimated heritabilities for the interval from birth to standing and from standing to apparently suckling to be between 0.08 and 0.22 in Merinos and Dorpers. In Suffolk sheep, the heritability of vigour (a score based on lamb behavioural progress immediately after birth) was 0.35 (MacFarlane *et al* 2010). Maternal effects are generally not significant for these traits (Cloete *et al* 2002) but the maternal environment to facilitate suckling plays a role in the neonatal progress of lambs (Cloete & Scholtz 1998; Kuchel & Lindsay 1999). For example, the interval from standing to apparently suckling is shorter in a Merino line selected for multiple-rearing ability than in a parallel line divergently selected against multiple-rearing ability. The line difference was partially accounted for by the inclusion of maternal co-operation with the first suckling attempts of the neonate in the model of analysis (Cloete & Scholtz 1998).

Lambs need to keep up with their dams soon after birth by showing appropriate locomotor competence, and the ability to discriminate their dam from other ewes. Studies in Merinos suggested that separation between ewe and lamb is a major contributory factor to lamb mortality (Stevens *et al* 1982; Alexander *et al* 1983), and that lamb factors are implicated in separations (Stevens *et al* 1984; O'Connor & Lawrence 1992). In tests, Merino lambs that could recognise their mothers 12 h after birth had better survival than lambs that could not (Nowak & Lindsay 1992). Breed differences in the ability of lambs to discriminate their mothers have been demonstrated (Shillito-Walser *et al* 1981; Pickup 2003; Coombs & Dwyer 2008), although how much is due to the behaviour of the lamb or the ewe is not known (Nowak 1991; Terrazas *et al* 2002).

Cold resistance

Cold resistance is another important determinant of lamb survival in many environments. Although newborn lambs are able to maintain body temperature in air temperatures below freezing, provided the lamb is dry (McCutcheon *et al* 1983), hypothermia of wet neonatal lambs may account for nearly half of all perinatal deaths (Houston & Maddox 1974). Hypothermia also causes a decrease in lamb sucking activity (Alexander & Williams 1966), so accelerating death from starvation as the limited reserves of the neonate lamb are rapidly diminished.

There is considerable variation in the ability of lambs of different breeds to maintain homeothermy after birth (Sykes *et al* 1976; Samson & Slee 1981; Slee & Springbett 1986; Dwyer & Morgan 2006). Heritability estimates for cold resistance range from 0.3 to 0.7 (Slee & Stott 1986; Wolff *et al* 1987; Slee *et al* 1991). In addition, a major gene associated with cold resistance has been identified (Slee & Simpson 1991; Simpson & Slee 1998). Birth coat depth and skin thickness both show significant genetic correlations with cold resistance (Slee *et al* 1991), confirming that they are important components of the maintenance of homeothermy in lambs by providing insulation. Although birth coat and bodyweight differences play a role in cold resistance, significant breed differences still remain once these components have been accounted for (Samson & Slee 1981). This difference is presumably related to the ability of different breeds to generate endogenous heat via non-shivering thermogenesis (Dwyer & Morgan 2006). The composition of maternal colostrum also contributes to the available lipids for neonatal metabolism. Although variation in lamb intake probably contributes most to variation in colostral energy supply, breed differences in colostrum lipid content may also play a role (Dwyer & Morgan 2006).

Physical adaptations

Ease of parturition

A prolonged labour increases the possibility of brain trauma and hypoxia in the neonate (Haughey 1993), impairs sucking, locomotor activity and thermoregulation in lambs (Eales & Small 1980; Haughey 1980; Bellows & Lammoglia 2000; Dwyer 2003; Dwyer & Morgan 2006), and can cause pain and exhaustion in the ewe. Differences in length of parturition between breeds (Alexander *et al* 1990b; Fahmy *et al* 1997; Cloete *et al* 1998; Dwyer & Lawrence 1998) and lines (Cloete & Scholtz 1998) suggest that there is some genetic variation for this trait. Heritability estimates are low at between 0.05 and 0.2 (Cloete *et al* 2002, 2003; MacFarlane *et al* 2010). However, ewes from a selection line developed from strains of sheep selected for visual aesthetic qualities (including traits such as prominent horns and shoulder width), had twice the number of assisted births compared to the control line in the same study (10 vs 5%, respectively; Lambe *et al* 2006). This implies that selection for some phenotypic traits (eg 'blockiness' in rams) has inadvertently led to their female offspring being unable to lamb without assistance.

Wool shedding

Feral and certain breeds of sheep, such as the Wiltshire Horn, tend to shed their wool, reducing the need for shepherding tasks such as shearing (Tierney 1978; Rathie *et al* 1994), which sheep are known to find stressful (Rushen 1996). Wool shedding also makes these breeds considerably less susceptible to blowfly strike than non-wool shedding breeds (Tierney 1978; Litherland *et al* 1992). Heat stress may also be reduced in wool-shedding breeds during winter housing or in early summer. The degree to which fleece loss occurs in some breeds (eg North Country Cheviot and Wiltshire Horn) is under genetic control (Conington 1990). The Easycare breed carry a fleece of up to 1–2 inches in length through the winter which they cast in the spring (Vipond 2006). From observation, it is clear that there is a major gene influencing the fleece shedding in the Easycare breed and it would therefore be an ideal candidate for molecular genetic studies.

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Conclusion and animal welfare implications

Several characteristics of sheep with important implications for animal welfare — particularly disease resistance and lamb survival traits — are under genetic control. Thus, some animals and breeds are better able to look after themselves and so require different levels of input from man to prevent welfare problems. Some breeds, especially those heavily selected for production characteristics and accustomed to receiving high levels of human intervention, are currently unsuited to low input management systems. If these animals are to be managed with lower inputs then changes in breeding programmes are required to prevent severe welfare problems.

Through the use of structured breeding programmes that include relevant, broader breeding goals, within-breed improvements can be made to improve animal welfare by better matching genotypes with changing farm environments. For example, using selective breeding to identify animals that require less handling at birth reduces stressful encounters with man during birth interventions, encouraging better maternal-offspring bonding at parturition and leading to higher rates of lamb survival. Having sheep with stronger maternal abilities, such as those of some hill breeds again increases the chances of survival and improves animal welfare.

Many of the adaptations described above will also improve the financial viability of farming systems by reducing production losses and veterinary costs. In particular, the tangible economic benefits from breeding for disease resistance (Nieuwhof & Bishop 2005; Conington *et al* 2008b) provide an incentive for their inclusion into breeding programmes. Improved lamb survival will improve weaning percentage, and it was shown by Conington *et al* (2004) to have a greater economic benefit compared to increasing litter size *per se*. Hence, the breeding programme for hill breeds used in the UK since 2000 includes number of lambs reared as a maternal breeding goal trait (Conington *et al* 2001). As lambs born into higher litter sizes have a lower survival rate (Conington *et al* 2004), this is an additional incentive to focus on sheep that are better able to rear what they produce. However, the inclusion of some of the behavioural adaptations may cost the farmer more to record than the perceived benefits accrued, despite the non-market (or 'public good') value of these adaptations. One way to address this is through some additional weighting to each breeding goal trait by both their market and non-market values (Olesen *et al* 2006) which is discussed further by D'Eath *et al* (2010).

Many traits, such as some aspects of disease resistance and lamb survival, could easily be incorporated into existing sheep breeding programmes from current data. Other traits may require additional resources to capture informative data for selection decisions. However, incorporating these traits into breeding programmes would improve animal welfare by reducing the possibility of the emergence of adverse correlated responses of selecting only for production traits.

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