

PERSPECTIVES ON ANIMAL BIOSCIENCES

A perspective on animal welfare of grazing ruminants and its relationship with sustainability

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ABSTRACT

Sustainability is a complex theorem driven through the optimisation of interconnected economic, social and environmental parameters. Balancing trade-offs between these three parameters is used to define a sustainable system, and while economic and, to a degree, environmental parameters can be numericised, making optimisation more defined, social parameters are often more complex. In livestock systems, animal welfare is held as a central pillar of sustainability, but due to its complex nature, indicators of welfare are in practice often restricted to negative nutritional/environmental/health domains (e.g. poor food quality, injuries/diseases) rather than the wider more complex 'behavioural' or 'mental state' domain indicators (e.g. expression of rewarding behaviours). This perspective discusses the potential synergies and trade-offs between animal welfare and economic, societal and environmental pillars of sustainability for grazing ruminant systems. Grazing is often considered more animal welfare-friendly than housed or feedlot type systems, especially in relation to the behavioural and mental state domains (BMSD) within a more 'natural' environment, as it may provide a positive experience to the animal. However, the welfare status of grazing ruminants can differ with factors such as management practices and environmental conditions greatly influencing nutritional/environmental/health domains of welfare, where a more 'controlled environment' can be efficacious. Animals that are not maintained at a good level of welfare will not express their productive potential, although improving welfare standards may lead to higher costs of production and therefore an economic break, as a critical component of sustainability, is often applied to what can be achieved on farm. Increasing animal performance is seen as an effective approach to reducing emissions intensity, which has been borne out by the lower methane intensity of high-yielding dairy housed herds, although there are important ethical concerns regarding BMSD of animal welfare and the marked restriction in environmental choices and in foraging behaviour (negative effect on behavioural interactions). However, consumers need to understand that implementing more 'natural' production systems with higher animal welfare standards can incur extra costs for producers, leading to higher output prices and also higher emissions per unit of product, which will require a reduction in consumption to reduce overall emissions.

Keywords: environmental trade-offs, farm productivity, Five Domains model, Five Freedoms, silvopastoral, societal needs, sustainable intensification, welfare assessment.

Introduction

Livestock farming, particularly of ruminants (sheep and cattle), is a major component of rural landscapes providing vital services to society through high-quality nutrition, soil health, land management for biodiversity and leisure activities, and supporting rural communities. However, it also polarises society, more so than ever, with debate over animal welfare, impact of animal product consumption on human health and on the environmental footprint of livestock production (Dumont *et al.* 2019). This debate is central to the sustainability of livestock farming systems with economic, environmental and social parameters, and trade-offs widely used to define sustainability (Purvis *et al.* 2019; Fig. 1).



Fig. 1. Diagram representing the three dimensions of sustainability.

Systems were initially called unsustainable when a resource became depleted so much so that it became unavailable to the system, or when a product of the system accumulated to a degree that prevented the functioning of the system. Now, the meaning of the term is much wider (Broom *et al.* 2013). A suitable definition of sustainability in the context of farming can be ‘the ability of an ecosystem to maintain ecological processes, functions, biodiversity and productivity into the future’ (Thompson 2009). Additionally, the acknowledgement of animal welfare and elimination of pain have become more prevalent issues, and are now central to the sustainability of farming (Peyraud and Mirabito 2019) and are being increasingly perceived as an integral element of overall food quality (Horgan and Gavinelli 2006). Retailers are also recognising animal welfare as a constituent aspect of product image and quality, which creates a need for reliable systems for on-farm monitoring of animal welfare status and providing guarantees on production conditions (Horgan and Gavinelli 2006). Animal welfare, as defined within the Five Freedoms (FAWC 1992), is not a single metric, with health and nutrition factors (e.g. freedom from hunger and thirst, freedom from discomfort, freedom from pain, injury and disease) often easier to numerically assess and define than more emotion/behavioural factors (e.g. freedom from fear and distress, and freedom to express normal behaviour). Animals may also experience other negative experiences that include anxiety, panic, frustration, anger, helplessness, loneliness, boredom or depression. These situation-related experiences reflect animals’ perceptions of their external circumstances, and these aspects of mental state are integrated into the Five Domains model of assessing animal welfare (Mellor 2016). Although they are elicited by threatening, cramped, barren and/or isolated conditions, they can often be replaced by positive affects when animals are kept with congenial others in spacious, stimulus-rich and safe environments that provide opportunities for them to engage in behaviours

they find rewarding (Mellor 2016), thus contributing to a positive welfare status recognised in the Behavioural and Mental State Domain (BMSD) as differentiated from the Nutritional, Environmental and Health Domain (NEHD).

The farming of animals is no longer viewed by consumers simply as a means of food production. Instead they are increasingly focused on ‘clean and green’ production, and these production systems are seen as fundamental to other key ‘sustainability’ goals, such as food safety and quality, safeguarding environmental protection, enhancing the quality of life in rural areas and the preservation of the countryside, and ensuring that animals are properly treated (Horgan and Gavinelli 2006). On a worldwide level, the World Organisation for Animal Health has embarked on an initiative to develop global animal welfare guidelines and standards, and as stated by Horgan and Gavinelli (2006), consumers demand higher standards of animal protection, and it is incumbent upon policy-makers and legislators to respond accordingly. With respect to the welfare of ruminant animals, in general, grazing is considered more BMSD animal welfare-friendly than housed or feedlot type systems due to ‘naturalness’ – ruminants evolved to graze/browse! Thus, in housed systems there would be a higher risk of negatively affecting behavioural interactions (e.g. frustration due to foraging drive being impeded). In grazing systems, ruminants have increased potential to express their natural behaviour, are usually less restricted in terms of space, and can roam and therefore exercise (Hennessy *et al.* 2020). However, the welfare status of grazing ruminants can differ with factors, such as management practices and environmental conditions. This can result in a disharmonisation between the NEHD and BMSD, where a housed more controlled environment can be efficacious in ensuring greater health outcomes. Furthermore, higher levels of production intensity can ensure a greater economic return and also a lower environmental footprint per unit of product. Therefore, it is important to identify the potential synergies and trade-offs with other components of sustainability. Thus, the aim of this perspective piece is to identify and discuss the relationship between animal welfare (both in terms of NEHD and BMSD) and economic, societal and environmental pillars of sustainability for grazing ruminant systems.

Potential benefits and drawbacks of grazing over housed ruminant production systems

Pasture grazed *in situ* is one of the most competitive and sustainable feeding systems for dairy cows globally because of a low environmental footprint, the potential for excellent animal welfare, and the relatively low cost in the production and utilisation of the feed (Wilkinson and Lee 2018). However, because of seasonal variation in grass production

and inclement weather conditions, cattle may have to be accommodated and/or fed off pasture (French *et al.* 2015). Furthermore, as a consequence of extensive genetic gains, our most productive dairy cows can no longer rely solely on pasture to deliver the required nutrient intake to match milk yield output (Wilkinson and Lee 2018). Although there can be no doubt that cows are motivated to graze, little work has thus far addressed the importance of grazing for cow welfare, particularly associated with the BMSD (Smid *et al.* 2020).

Welfare is thought to be more negatively affected if an animal is denied access to a resource for which it is highly motivated. The inability to engage in natural feeding behaviours is associated with the development of stereotypical and other abnormal behaviours in many animal species (Smid *et al.* 2020). Animals in impoverished environments with severe restrictions or prevented from performing exploratory or foraging activities represent a clear reduction in welfare (Mellor 2015). In a survey of small holdings in Kerala, India, it was shown that cattle on farms that restricted access to forage/grazing showed a tongue rolling stereotypy that was absent in those with greater access to forage/grazing (Mullan *et al.* 2020). In more intensive production systems, given the option, cows appear to prefer access to pasture over access to a free-stall barn, but this preference is complex and is sometimes reversed depending on environmental conditions (von Keyserlingk *et al.* 2009; Shepley *et al.* 2017a, 2017b). Extremely pertinent to this debate is whether animals 'miss' something they have not experienced. (Rutter 2010). Cows that had not previously grazed to any great extent choose to go indoors almost twice as often as to pasture (66% vs 34%, respectively) and spent more time indoors compared with pasture (92% vs 8%, respectively), particularly high-yielding cows, suggesting they did not 'miss' having access to pasture (Rutter 2010; Charlton *et al.* 2011). Furthermore, summer grazing has a positive impact on animal behaviour, but this beneficial effect is temporary (i.e. not maintained during the indoor period; Corazzin *et al.* 2010) and variable among herds (mainly due to differences in duration of access to pasture and quality of herd management; Burow *et al.* 2013). If this is the case, Rutter (2010) suggests it might be better for their welfare if cattle are kept either permanently indoors or permanently outdoors, rather than switching between environments. On the contrary, Mee and Boyle (2020) stress that at the extremes of management systems, there can be major differences in animal welfare, but in hybrid systems, dairy cows experience elements of both confinement and pasture that may ameliorate the negative effects of each on cow welfare and differentiate for the need to deliver all aspects of the Five Freedoms (FAWC 1992). Nevertheless, there are other interconnected factors that need to be considered when selecting the optimal 'sustainable' system; that is, trade-offs between animal welfare, economics and the environment.

With respect to the NEHD, it is often perceived that more controlled environments from housed systems would improve the detection and amelioration of disease and nutritional inadequacies. Potential areas of greater concern for health welfare within pasture-based systems may include physiological indicators of more severe negative energy balance, greater risk of internal parasitism, malnutrition (especially micronutrients), delayed onset of oestrous activity postpartum, and in some situations, the potential for compromised welfare with exposure to unpredictable and extreme weather conditions (Fisher and Webster 2013; Arnott *et al.* 2017; Mee and Boyle 2020). These issues have been particularly observed in extensive systems with beef calves (Hemsworth *et al.* 1995) and sheep (Munoz *et al.* 2018). In these production systems, problems regarding the animals' NEHD welfare and subsequently their BMSD welfare may arise from several issues, such as decreased forage availability, forage nutrient deficiencies, lack of access to water and shelter, inappropriate stable installations, inadequate veterinarian care, and so on (Koidou *et al.* 2019). In Danish production settings, available farmland close to cow barns is typically scarce, and cows often have to walk long distances on stony and/or muddy tracks between milking and grazing, increasing the risk of lameness, as well as increasing man hours and labour (Otten *et al.* 2016). Thus, grazing was excluded from The Danish Act on Keeping of Dairy Cattle and their Offspring (LBK no 58 11/01/2017), and it was compensated with more space indoors (Otten *et al.* 2020). Also, welfare issues can arise under heat stress conditions (Galán *et al.* 2018). However, in general, issues that relate to lower standards of the NEHD of welfare at pasture align to substandard animal husbandry or farm resources, although meteorological events are not within the control of the farmer. As grazing systems are often associated with a lower level of intensity and, therefore, metabolic stress on the animal, cows on pasture-based systems typically have been shown to have lower levels of lameness, hoof pathologies, hock lesions, mastitis, uterine disease, ruminal acidosis (SARA and acute) and mortality compared with cows in continuously housed systems (Meul *et al.* 2012; de Vries *et al.* 2015; Arnott *et al.* 2017; Sjöström *et al.* 2018). Pasture access also benefits dairy cow behaviour, in terms of grazing, improved lying/resting times, lower levels of aggression, more normal oestrous behaviours and better synchronicity of behaviours than confined cows (Arnott *et al.* 2017; Wagner *et al.* 2018; Mee and Boyle 2020). Also, grazing has been reported to positively affect 'expression of social behaviours,' and 'positive emotional state' delivering to the BMSD of animal welfare (Wagner *et al.* 2018). Young calves that stay outdoors on grass increase their exposure to stimuli given by fresh air, light, natural surroundings, space and changing weather conditions, providing conditions that enable the calf to fully express its natural rewarding behaviour (Vaarst *et al.* 2001).

Grazing is not a guarantee for high welfare in any domain of animal welfare; equally, housing does not necessarily lead to lower welfare in the NEHD, although delivering BMSD welfare is more challenging (Burow *et al.* 2013). Beneficial effects are not realised when management does not satisfy the animals' needs (Wagner *et al.* 2018), and management may be as important as the system type (grazing, indoor, hybrid) in ensuring good dairy cow welfare and addressing societal concerns (Mee and Boyle 2020).

Animal welfare of grazing ruminants, and its relationship with economic performance and productivity

Besides the fact that high animal welfare is a critical standard to be upheld by the livestock farming industry, animals that are not maintained to a high level of welfare may not express their productive potential (Arraño *et al.* 2007). Therefore, it seems logical to provide animals with the highest standards of welfare possible. However, this will lead to higher costs of production, which may soon reach a plateau for return on investment over enhanced performance. Although, win–wins where higher animal welfare delivers cost savings should be sought; for example, extending the grazing season can increase the economic performance of a farm (French *et al.* 2015), as well as the BMSD welfare status (Burow *et al.* 2013). Moreover, grass-based production systems have been used as a marketing approach by retailers and processors, as consumers perceive pasture-based systems as more 'natural' and, therefore, better for cow welfare and the environment (Shortall 2019). In fact, this positive perception has been harnessed by farming groups and encouraged by governments (Wilkinson *et al.* 2020). Programmes, such as 'Milk from Happy Cows' (Leite de Vacas Felizes; Vasconcelos 2019) and 'Pasture for life' (<https://www.pastureforlife.org/>), have been launched promoting grazing, and highlighting the numerous benefits to human health, environment and animal welfare, while farmers receive a better price for their produce. Given this higher return per litre of milk, for instance in 'Milk from Happy Cows', farmers are encouraged to invest more in their farms, better manage their grasslands, adopt more sustainable farming practices and improve animal welfare (Vasconcelos 2019). These products can be differentiated through special labels, and consumers can access accurate information about the production conditions, as traceability and transparency are highly appreciated by consumers (Arraño *et al.* 2007). It has also been reported that housed systems, as opposed to pasture-based dairy systems, may reduce udder health by increasing somatic cell counts. Although this is likely to be an indirect function of the breeds and metabolic stress driven by higher yield requirements rather than housing *per se*, the resulting higher

somatic cell counts would reduce revenue through milk price penalties for the lower hygienic quality (Arnott *et al.* 2017).

Synergies between animal welfare and farm productivity are not constrained to just the dairy sector, with meat (both beef and sheep) being marketed as pasture-based to take advantage of the consumers' perception of 'naturalness' and 'quality'. Other economic advantages of pasture-based systems can also be found over and above the cost of feeding and perception of product quality. For example, a novel system combining hill sheep production with native woodland creation has been established in a Scottish mountain valley (Morgan-Davies *et al.* 2008). This mixed system provides shelter for animals, and better-quality grazing in spring and early autumn; that is, improving animal welfare, and producing more kilograms of lamb per ewe and higher margins than a hill-grassland only. Additionally, there is extra income from the timber and a carbon off-setting value, which can be materialised economically through carbon credits or environmentally through carbon capture (if the trees are not used for fuel) and soil health.

Interventions to increase systems performance or revenues can also cause a reduction in animal welfare. Winter lambing is practised in some parts of New Zealand, to provide lambs in spring when prices are highest. However, lambs born outside spring are usually lighter than spring-born lambs, and the lambing percentage is also lower. Furthermore, milk production is lower in ewes lambing outside spring, resulting in their lambs growing slower, with mortality subsequently higher than spring-born lambs (Stafford and Gregory 2008). High herd mortality levels indicate suboptimal NEHD welfare conditions, and death is likely preceded by a period of suffering and is therefore a potential wider BMSD welfare concern; that is, freedom from fear and distress (Arnott *et al.* 2017), and lack of the positive feeling of healthiness (Mellor 2016). A further example of the trade-offs between economic efficiency and animal welfare is the legislations that have determined the minimal area required per animal in livestock housing facilities, which has increased production cost for a given level of product (Dumont *et al.* 2019). The building costs can be drastically reduced by outdoor wintering of cattle. However, in some countries, such as Sweden, the tradition of indoor wintering of all cattle and strict animal welfare legislation make cheap outdoor wintering difficult to achieve, even if meteorologically possible, which of course is not always the case (Kumm 2014).

Maintaining profitability is a challenge for any business, as decreasing returns and increasing costs squeeze profits, especially in a sector that in certain parts of the world; for example, Europe relies heavily on subsidy. This can lead to larger operations benefiting from economies of scale evident in larger farms, flocks and herd sizes (Fisher 2020). Expansion is also seen as a welfare risk, such as a lack of investment in farm infrastructure required to improve

welfare as farm sizes increase (Shortall 2019). Therefore, it is important to know the costs of improving animal welfare as farms increase in size and how these extra costs might be distributed across the food supply chain, as well as how this impacts the consumer. Taxes and subsidies are one option often used to ensure standards, with some countries linking subsidies to successful animal welfare inspections. Improvements to animal welfare can also be market driven, but historically there has been lack of economic incentive to accompany the ethical argument to improve animal welfare (Fernandes *et al.* 2019). One option to overcome this lack of incentive is labelling products (e.g. 'Milk from Happy Cows', 'Pasture for life') from preferred animal welfare-friendly systems, which would enable motivated consumers to support them (Fisher 2020). Nevertheless, this premium price for labelled products may not compensate fully for the increased costs associated with delivering the required animal welfare standards; for example, additional labour, a lower annual milk yield per cow, use of additional straw, large grazing area and, therefore, less area for on-farm feed production (Oudshoorn *et al.* 2011). The economic theory of demand suggests that people's preferences for 'welfare-friendly' products may not be particularly responsive to prices. However, as preferences change with increasing food security, education, awareness and ability to exercise choice in consumer goods selection, animal welfare preferences are likely to rise with income levels – and also with changing information and attitudes over time. However, there will be a range of valuations attached to the welfare characteristics of livestock products, some people valuing them highly, whereas for others they confer no perceived benefit (McInerney 2004). Therefore, although positive welfare is positioned as a marketing advantage, there are calls for vitally needed research and industry initiatives to demonstrate and improve animal welfare as the sector expands (Shortall 2019). This is particularly important where economic efficiency is subordinate to animal welfare; that is, net profit per farm is lower for an 'enhanced welfare scenario' than in a 'business as usual scenario', as the system is driven by economic incentives and implemented new technologies and measures are aimed at enhancing productivity and efficiency (Oudshoorn *et al.* 2011). However, it is also important to emphasise that increasing yield does not always deliver higher profits; this is particularly true when there is a reliance on commodity-based feeds (e.g. soya and grain) to deliver to the enhanced requirements of an intensive production system.

As concluded by Dawkins (2017), the potential conflicts between animal welfare and efficient farming can often be resolved or at least reduced by showing the financial benefits that improving animal welfare can bring via: (1) reduced mortality; (2) improved health; (3) improved product quality; (4) improved disease resistance and reduced medication; (5) lower risk of zoonoses and foodborne

diseases; (6) farmer job satisfaction and contributions to Corporate Social Responsibility; and (7) the ability to command higher prices from consumers. However, higher animal welfare standards often come at a greater financial cost to the farm system (Fisher 2020). Some may be one-time costs associated with changing infrastructure and switching practices, some may be ongoing operational costs, and some may be costs to which all businesses in an industry must contribute indirectly (Fernandes *et al.* 2021). Whichever the cost is, its impact on the profitability of the business should be considered in addition to the level of improvement potentially to be achieved with the implementation of the change.

Animal welfare of grazing ruminants and its relationship with environmental impact

If animals are able to optimise their own efficiency of nutrient capture, there could be significant environmental benefits in allowing animals to select their own diets; each unit of animal product requires less feed input, reducing the direct (both financial and environmental) and indirect (transporting feed to the animal) costs. Additionally, improved nutrient use efficiency results in less pollution from excreted waste nutrients and improves the ratio of unit production per unit pollution (Rutter 2010). This would suggest that it is possible that facilitating the self-selection of diets in ruminant livestock; that is, expressing their rewarding behaviour, could result in a significant reduction in the environmental pollution arising from livestock agriculture. However, pasture is not a perfect 'bag of nutrients' (protein, energy and micronutrients) required to deliver the level of performance we expect from our genetically improved livestock. This often means that pasture-based production alone will fail to deliver a required milk yield or average daily gain, which has seen an increase in in-parlour supplementation or total mixed ration diets (Wilkinson and Lee 2018). The feeding system is therefore tuned to meet the 'new' genetic potential of the animal. Increasing animal performance is seen as an effective approach to reducing emissions per unit of product (emissions intensity). Increasing yields further from their current levels would require further genetic improvement, which aligns to greater nutrient requirements. Thus, higher genetic merit cows will produce more milk, but also produce more enteric methane, because their feed intake is higher. Although the methane emissions per litre of milk are often lower, as the requirement for maintenance of the animal is offset through higher levels of performance per animal. It is notable that the emissions intensity of a fully housed dairy was approximately 18.5% lower than cows that graze for 9 months of the year (CIEL 2020). Although, it must be recognised that this figure of emissions intensity does not

include the wider carbon-offsetting potential of the production systems (see below in relation to soil health), which is important when comparing pasture-based versus intensive housed systems. However, even when considering carbon-offsetting of pasture-based systems, it has been predicted that in an 'animal welfare scenario', emissions of greenhouse gases and energy use per kg milk is higher than in a 'business as usual scenario' (Oudshoorn *et al.* 2011). Yet there are also important ethical concerns regarding animal welfare related with overexploitation of cows for yield (Morais *et al.* 2018). Therefore, adoption of a system that resulted in a higher emissions intensity, but was perceived as preferable in terms of other parameters of sustainability (e.g. BMSD of welfare), would require lower levels of consumption, and therefore production, to meet the same total environmental impact in terms of greenhouse gas emissions. Under this scenario, economic sustainability would only be delivered if the consumer was willing to pay more for less of a product produced in a certain way.

There are also synergies between animal welfare and environment, as particularly observed in silvopastoral systems. These mixed systems have been shown to improve both animal welfare and biodiversity (Morgan-Davies *et al.* 2008). Silvopastoral systems that combine livestock and trees offer two main advantages for the animals: trees modify microclimatic conditions, which can have beneficial effects on pasture growth and animal welfare, and also provide alternative feed resources during periods of low forage availability (Smith *et al.* 2012). Silvopastoral systems improve animal welfare by allowing animals to browse and acquiring nutritionally rich diets (Mejía-Díaz *et al.* 2016; Broom 2017), favouring the social stability of the herd and the expression of semipositive behaviours (i.e. behaviours that are known to reflect positive affective states; Améndola *et al.* 2016), promoting more interspersed idleness, rumination and grazing activities (Carnevalli *et al.* 2020), increasing comfort and diversifying the environment (Morales *et al.* 2017), reducing stress (Marques Filho *et al.* 2017), providing shade for thermal comfort (Vieira *et al.* 2020), reducing the fear response (Broom *et al.* 2013), and improving body condition (Mancera *et al.* 2018), among other benefits. The integrated crop–livestock–forest systems also improve the microclimate conditions, mitigating the heat through trees and contributing to the sustainability of livestock farming in the tropics with direct effect on welfare and thermal comfort (Broom *et al.* 2013; Karvatté *et al.* 2016). Agroforestry/silvopastoral systems also have wider environmental benefits associated with nutrient distribution and soil health. In an open pasture, it has been shown that heifers search for drinkers and then spend most of their time camping around these sites (Carnevalli *et al.* 2020), thus creating hot spots of nutrients and soil compaction, and increasing emissions of nitrous oxide, a potent greenhouse gas. In contrast, within silvopastoral

systems, heifers camp across a wider area under trees in the shade reducing nutrient hotspots and compaction. Water, salt, and mineral and protein supplements can be used as attractants to improve the livestock distribution on pastures without trees, and grazing uniformity on grasslands will reduce compaction and emissions of nitrous oxide (Oenema *et al.* 1997; Koidou *et al.* 2019).

There is no doubt that the return of organic carbon to soils is of great benefit to the planet through removing carbon dioxide from the atmosphere and improving biological functioning of soil (Neal *et al.* 2020). Prout *et al.* (2021) used a soil organic carbon:clay ratio to investigate the organic carbon status of UK soils across various land uses (arable, grassland and forest). Using this ratio, they showed that that 40% of arable soils were degraded; that is, they had a low soil organic carbon:clay ratio, whereas only 7% of grassland soils were degraded, a figure comparable to forest soils that are in good soil health. Notwithstanding soil as a potential carbon capture approach, increasing soil carbon storage improves overall soil health (biological functioning) and water-holding capacity through improved physical microscale structure. Therefore, increasing soil organic carbon will contribute to net zero carbon targets either directly (carbon capture) or indirectly (soil health) and help reduce the risk of flash floods. The world's longest running experiments at Rothamsted Research in the UK, the classical long-term experiments (some over 175 years), demonstrate that animal manures and grasslands are the best approach to return carbon and, therefore, health to soil (Poulton *et al.* 2018). Thus, it is clear that there may be positive and negative interactions between welfare and environmental impact with respect to grazing, and these effects should be assessed comprehensively to determine the overall effect.

Animal welfare of grazing ruminants and its relationship with societal needs

The overarching societal need from livestock systems is delivering accessible high-quality nutrition. Grazed pasture, as opposed to housed systems, generally leads to increased levels of beneficial fats in milk and meat; for example, polyunsaturated fatty acids, especially omega-3 polyunsaturated fatty acids, and conjugated linoleic acid, which would increase the nutritional value of the product (Wilkinson *et al.* 2020). As well as changes in fat profiles, O'Callaghan *et al.* (2016) showed that grazing resulted in higher concentrations of total protein and casein, and Manzi and Durazzo (2017) reported higher concentrations of fat-soluble vitamins (β -carotene and α -tocopherol) in pasture-based organic milk than conventional milk, improving the 'health' quality of the milk. However, although the profile is enhanced nutritionally, the differences were

negligible at the level of standard milk servings (EFSA 2017). Detrimently, Manzi and Durazzo (2017) reported a significant reduction in iodine concentration in pasture-based organic milk compared with conventional milk. This is likely related to conventional cows receiving minerals containing supplementary iodine and selenium, which is involved in iodine metabolism. Pastures are often found to contain relatively low levels of iodine and selenium (Kao *et al.* 2020). Furthermore, in diverse swards, which may be favoured in organic systems, animals may be more at risk to plant-based iodine antagonists, such as glucosinolates.

As already mentioned, production methodology is an important aspect of animal-based products, with pasture-based marketed for its naturalness with perceived delivery of animal welfare, nutritional quality and lower environmental footprint. Milk suppliers (supermarkets and milk processors) are targeting the more discerning consumer via marketing grazing and grass-based systems of milk production at a premium, as exemplified by the organic movement. Such strategies rely on the consumer recognising, seeking out and valuing such commitments at a level that they are willing to pay more for what is in essence a similar product to milk produced from housed cows. However, societal need is not just for the discerning consumer, who can afford to make a choice to pay more. Societal need for high-quality nutrition must deliver for all and cater for poorer income households, which would position cheaper, more intensive milk from housed cows as a more socially sustainable product.

However, grazing livestock also provide other societal needs reflected in rural access, countryside stewardship, landscape aesthetics and supporting rural communities. Livestock grazing is at the heart of most rural communities, utilising land that is not suitable for any other form of food production, providing jobs and countryside that can provide mental relaxation for urban and rural visitors alike. Grassland countryside is more accessible for leisure and tourism than arable agriculture, which ultimately provides feed for housed cattle production systems, as well as directly for human consumption and indirectly for other livestock sectors; for example poultry. Although, there have been moves as to the value of re-wilding and removing livestock from grasslands, which would arguably deliver more land for countryside pursuits, and further improve mental wellbeing via greater access to the countryside for an increasingly stressed population. However, this conversion would put rural communities at risk, as although leisure and tourism businesses would replace, to an extent, agricultural businesses (farms), the more variable nature and seasonality of this sector may not be enough to cover the income gap.

Although the welfare of most animals reflects the care provided by those in charge of them, it is influenced by the wider community, and thus subject to contested scrutiny. Therefore, is society, by influencing animal welfare standards, at risk of disregarding the invaluable perspectives of those

husbanding animals, who are best placed to understand the animals in their care, and their societal need? (Fisher 2020). Animal welfare is a natural process that needs to be expressed as well as possible to develop sustainable, efficient farming practices that will allow the farmer to feel their work is valued (Peyraud and Mirabito 2019). As described by Fisher (2020) it is perhaps more relevant to think of animal welfare in terms of a system (Fig. 2), as humans and animals are socially and ecologically interdependent. At the centre of the system are animals; then there are the persons in charge (i.e. farmers and farm workers); those with oversight of the persons in charge (i.e. animal welfare inspectors and regulatory advisory bodies); and those with an interest in animals (i.e. consumers of food, commerce interests, and animal advocates and activists). Finally, there are citizens, who, although not necessarily having direct vested interests in animals, have a special role in the democratic process. This highlights the complexity that the supply chain and the whole of society face when it comes to agreeing on the standards of animal welfare and their implementation.

Conclusion

All actions aimed towards sustainability must take account of every aspect that defines a sustainable system. If the focus of an action were to be entirely on animal welfare or a component of welfare; for example health, some other harm might be done (Broom 2019). Thus, the question that inevitably derives from this complex reality is: how can we assess systems simultaneously in relation to animal welfare and the wider economic, environmental and social dimensions of sustainability? It is clear that not all of the metrics can be maximised, as there are trade-offs. However systems can be improved to obtain the highest levels of overall sustainability through an aggregate sustainability score, provided that there are minimum levels (red lines, e.g. a

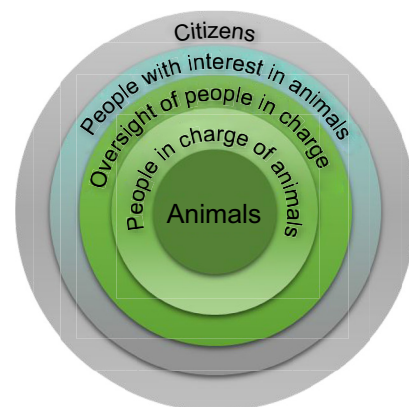


Fig. 2. A schematic representation of the animal welfare system [adapted from Fisher *et al.* (2014)].

welfare standard or level of biodiversity) guaranteed for each element comprising the different pillars. Galioto *et al.* (2017), proposed a multi-attribute hierarchical evaluation model for the evaluation of the aggregate sustainability of livestock farms integrating the economic, environmental and social aspects. They measured sustainability using indicators, including carbon footprint, farm income and animal welfare, where the weight of each element is the subjective component of the assessment criterion. It seems that agreeing on weighing and establishing adequate records for the objective measures could be the most relevant steps towards assessing grazing livestock systems on their overall sustainability.

References

- Améndola L, Solorio FJ, Ku-Vera JC, Améndola-Massiotti RD, Zarza H, Galindo F (2016) Social behaviour of cattle in tropical silvopastoral and monoculture systems. *Animal* **10**, 863–867. doi:10.1017/S1751731115002475
- Arnott G, Ferris CP, O'connell NE (2017) Review: welfare of dairy cows in continuously housed and pasture-based production systems. *Animal* **11**, 261–273. doi:10.1017/S1751731116001336
- Arraño C, Báez A, Flor E, Whay HR, Tadich N (2007) Estudio preliminar del uso de un protocolo para evaluar el bienestar de vacas lecheras usando observaciones basadas en el animal. *Archivos de medicina veterinaria* **39**, 239–245. doi:10.4067/s0301-732x2007000300007
- Broom DM (2017) Components of sustainable animal production and the use of silvopastoral systems. *Revista Brasileira de Zootecnia* **46**, 683–688. doi:10.1590/S1806-92902017000800009
- Broom DM (2019) Animal welfare complementing or conflicting with other sustainability issues. *Applied Animal Behaviour Science* **219**, 104829. doi:10.1016/j.applanim.2019.06.010
- Broom DM, Galindo FA, Murgueitio E (2013) Sustainable, efficient livestock production with high biodiversity and good welfare for animals. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20132025. doi:10.1098/rspb.2013.2025
- Burow E, Rousing T, Thomsen PT, Otten ND, Sørensen JT (2013) Effect of grazing on the cow welfare of dairy herds evaluated by a multidimensional welfare index. *Animal* **7**, 834–842. doi:10.1017/S1751731112002297
- Carnevali RA, de Mello ACT, Coletti AJ, Garcia LF, Xavier DB (2020) Shade controls the ruminating and idleness times of dairy heifers in tropical integrated systems. *Agroforestry Systems* **94**, 779–790. doi:10.1007/s10457-019-00448-7
- Charlton GL, Rutter SM, East M, Sinclair LA (2011) Preference of dairy cows: indoor cubicle housing with access to a total mixed ration vs. access to pasture. *Applied Animal Behaviour Science* **130**, 1–9. doi:10.1016/j.applanim.2010.11.018
- CIEL (2020) Net zero carbon & UK livestock. 57. <https://www.cielivestock.co.uk/net-zero-carbon-and-uk-livestock/>.
- Corazzin M, Piasentier E, Dovier S, Bovolenta S (2010) Effect of summer grazing on welfare of dairy cows reared in mountain tie-stall barns. *Italian Journal of Animal Science* **9**, 304–312. doi:10.4081/ijas.2010.e59
- Dawkins MS (2017) Animal welfare and efficient farming: is conflict inevitable? *Animal Production Science* **57**, 201–208. doi:10.1071/AN15383
- de Vries M, Bokkers EAM, van Reenen CG, Engel B, van Schaik G, Dijkstra T, de Boer IJM (2015) Housing and management factors associated with indicators of dairy cattle welfare. *Preventive Veterinary Medicine* **118**, 80–92. doi:10.1016/j.prevetmed.2014.11.016
- Dumont B, Ryschawy J, Duru M, Benoit M, Chatellier V, Delaby L, Donnars C, Dupraz P, Lemauviel-Lavanant S, Méda B, Vollet D, Sabatier R (2019) Review: associations among goods, impacts and ecosystem services provided by livestock farming. *Animal* **13**, 1773–1784. doi:10.1017/S1751731118002586
- EFSA (2017) Dietary reference values for nutrients summary report. *EFSA Supporting Publications* **14**, e15121E. doi:10.2903/sp.efsa.2017.e15121
- FAWC (1992) Farm Animal Welfare Council updates the five freedoms. *Veterinary Record* **17**, 357.
- Fernandes J, Blache D, Maloney SK, Martin GB, Venus B, Walker FR, Head B, Tilbrook A (2019) Addressing animal welfare through collaborative stakeholder networks. *Agriculture (Switzerland)* **9**, 132. doi:10.3390/agriculture9060132
- Fernandes JN, Hemsworth PH, Coleman GJ, Tilbrook AJ (2021) Costs and benefits of improving farm animal welfare. *Agriculture (Switzerland)* **11**, 104. doi:10.3390/agriculture11020104
- Fisher MW (2020) Pastoral farming ethics and economics – aligning grazing practices and expectations. *Frontiers in Veterinary Science* **7**, 1–12. doi:10.3389/fvets.2020.00209
- Fisher AD, Webster JR (2013) Dairy cow welfare: the role of research and development in addressing increasing scrutiny. *Animal Production Science* **53**, 924–930. doi:10.1071/AN12276
- Fisher M, Diesch T, Orange M (2014) Scapegoats and tourists – science as the source of, and the answer to, ethical dilemmas. In 'Mixing it up – ethics, science and adventure tourism'. (Eds G Sutherland, P Cragg) pp. 2–7. (ANZCCART: Wellington)
- French P, Driscoll KO, Horan B, Shalloo L (2015) The economic, environmental and welfare implications of alternative systems of accommodating dairy cows during the winter months. *Animal Production Science* **55**, 838–842. doi:10.1071/AN14895
- Galán E, Llonch P, Villagrà A, Levit H, Pinto S, del Prado A (2018) A systematic review of non-productivity related animal-based indicators of heat stress resilience in dairy cattle. *PLoS ONE* **13**, e0206520. doi:10.1371/journal.pone.0206520
- Galioto F, Paffarini C, Chiorri M, Torquati B, Cecchini L (2017) Economic, environmental, and animal welfare performance on livestock farms: conceptual model and application to some case studies in Italy. *Sustainability (Switzerland)* **9**, 1615. doi:10.3390/su9091615
- Hemsworth PH, Barnett JL, Beveridge L, Matthews LR (1995) The welfare of extensively managed dairy cattle: a review. *Applied Animal Behaviour Science* **42**, 161–182. doi:10.1016/0168-1591(94)00538-P
- Hennessy D, Delaby L, van den Pol-van Dassel A, Shalloo L (2020) Increasing grazing in dairy cow milk production systems in Europe. *Sustainability (Switzerland)* **12**, 2443. doi:10.3390/su12062443
- Horgan R, Gavinelli A (2006) The expanding role of animal welfare within EU legislation and beyond. *Livestock Science* **103**, 303–307. doi:10.1016/j.livsci.2006.05.019
- Kao PT, Darch T, McGrath SP, Kendall NR, Buss HL, Warren H, Lee MRF (2020) Factors influencing elemental micronutrient supply from pasture systems for grazing ruminants. In 'Advances in agronomy, Vol. 164'. (Ed. A Sparks) pp. 161–229. (Academic Press: Cambridge, MA). doi:10.1016/bs.agron.2020.06.004
- Karvátte Jr N, Klosowski ES, de Almeida RG, Mesquita EE, de Oliveira CC, Alves FV (2016) Shading effect on microclimate and thermal comfort indexes in integrated crop–livestock–forest systems in the Brazilian Midwest. *International Journal of Biometeorology* **60**, 1933–1941. doi:10.1007/s00484-016-1180-5
- Koidou M, Mountousis I, Dotas V, Zagorakis K, Yiakoulaki M (2019) Temporal variations of herbage production and nutritive value of three grasslands at different elevation zones regarding grazing needs and welfare of ruminants. *Archives Animal Breeding* **62**, 215–226. doi:10.5194/aab-62-215-2019
- Kumm K-I (2014) Achieving profitable, productive climate-neutral Swedish agriculture. *Outlook on Agriculture* **43**, 247–252. doi:10.5367/oa.2014.0182
- Mancera KF, Zarza H, de Buen LL, García AAC, Palacios FM, Galindo F (2018) Integrating links between tree coverage and cattle welfare in silvopastoral systems evaluation. *Agronomy for Sustainable Development* **38**, 223. doi:10.1007/s13593-018-0497-3
- Manzi P, Durazzo A (2017) Organic vs. conventional milk: some considerations on fat-soluble vitamins and iodine content. *Beverages* **3**, 39. doi:10.3390/beverages3030039
- Marques Filho WC, Barbosa GF, Cardoso DL, Ferreira AD, Pedrinho DR, Bono JAM, de Souza CC, Frainer DM (2017) Productive sustainability in a silvopastoral system. *Bioscience Journal* **33**, 10–18. doi:10.14393/bj-v33n1a2017-32925

- McInerney JP (2004) Animal welfare, economics and policy. Available at <https://webarchive.nationalarchives.gov.uk/ukgwa/20110318142209/http://www.defra.gov.uk/evidence/economics/foodfarm/reports/documents/animalwelfare.pdf>. [Accessed 11 February 2022]
- Mee JF, Boyle LA (2020) Assessing whether dairy cow welfare is “better” in pasture-based than in confinement-based management systems. *New Zealand Veterinary Journal* **68**, 168–177. doi:10.1080/00480169.2020.1721034
- Mejía-Díaz E, Mahecha-Ledesma L, Angulo-Arizala J (2016) *Tithonia diversifolia*: especie para ramoneo en sistemas silvopastoriles y métodos para estimar su consumo. *Agronomía Mesoamericana* **28**, 289. doi:10.15517/am.v28i1.22673
- Mellor DJ (2015) Positive animal welfare states and encouraging environment-focused and animal-to-animal interactive behaviours. *New Zealand Veterinary Journal* **63**, 9–16. doi:10.1080/00480169.2014.926800
- Mellor DJ (2016) Updating animalwelfare thinking: Moving beyond the “five freedoms” towards “A lifeworth living”. *Animals* **6**, 21. doi:10.3390/ani6030021
- Meul M, Van Passel S, Fremaut D, Haesaert G (2012) Higher sustainability performance of intensive grazing versus zero-grazing dairy systems. *Agronomy for Sustainable Development* **32**, 629–638. doi:10.1007/s13593-011-0074-5
- Morais TG, Teixeira RFM, Rodrigues NR, Domingos T (2018) Carbon footprint of milk from pasture-based dairy farms in Azores, Portugal. *Sustainability (Switzerland)* **10**, 3658. doi:10.3390/su10103658
- Morales AMT, Ceballos MC, Londoño GC, Cardona CAC, Ramírez JFN, da Costa MJRP (2017) Welfare of cattle kept in intensive silvopastoral systems: a case report. *Revista Brasileira de Zootecnia* **46**, 478–488. doi:10.1590/S1806-92902017000600002
- Morgan-Davies C, Waterhouse A, Pollock ML, Holland JP (2008) Integrating hill sheep production and newly established native woodland: achieving sustainability through multiple land use in Scotland. *International Journal of Agricultural Sustainability* **6**, 133–147. doi:10.3763/ijas.2007.0248
- Mullan S, Bunglavan SJ, Rowe E, Barrett DC, Lee MRF, Ananth D, Tarlton J (2020) Welfare challenges of dairy cows in India identified through on-farm observations. *Animals* **10**, 586. doi:10.3390/ani10040586
- Munoz C, Campbell A, Barber S, Hemsworth P, Doyle R (2018) Using longitudinal assessment on extensively managed ewes to quantify welfare compromise and risks. *Animals* **8**, 8. doi:10.3390/ani8010008
- Neal AL, Bacq-Labreuil A, Zhang X, Clark IM, Coleman K, Mooney SJ, Ritz K, Crawford JW (2020) Soil as an extended composite phenotype of the microbial metagenome. *Scientific Reports* **10**, 4997. doi:10.1038/s41598-020-67631-0
- O’Callaghan TF, Hennessy D, McAuliffe S, Kilcawley KN, O’Donovan M, Dillon P, Ross RP, Stanton C (2016) Effect of pasture versus indoor feeding systems on raw milk composition and quality over an entire lactation. *Journal of Dairy Science* **99**, 9424–9440. doi:10.3168/jds.2016-10985
- Oenema O, Velthof GL, Yamulki S, Jarvis SC (1997) Nitrous oxide emissions from grazed grassland. *Soil Use and Management* **13**, 288–295. doi:10.1111/j.1475-2743.1997.tb00600.x
- Otten ND, Rousing T, Houe H, Thomsen PT, Sørensen JT (2016) Comparison of animal welfare indices in dairy herds based on different sources of data. *Animal Welfare* **25**, 207–215. doi:10.7120/09627286.25.2.207
- Otten ND, Rousing T, de Oliveira VHS, Reiten M, Michelsen A-M, Hakansson F, Lund VP, Houe H, Denwood M, Sørensen JT, Forkman B, Kirchner MK (2020) A weak point analysis of welfare in Danish dairy herds using two different welfare assessment systems. *Animal Welfare* **29**, 197–207. doi:10.7120/09627286.29.2.197
- Oudshoorn FW, Sørensen CAG, de Boer IJM (2011) Economic and environmental evaluation of three goal-vision based scenarios for organic dairy farming in Denmark. *Agricultural Systems* **104**, 315–325. doi:10.1016/j.agry.2010.12.003
- Peyraud J-L, Mirabito L (2019) Initiatives and achievements by farmers and the livestock sector in favour of animal welfare. In ‘Introduction: livestock breeding in France and animal welfare’. (Eds S Hild, L Schweitzer) pp. 141–153. (Animal Welfare: From Science to Law: Paris, France)
- Poultou P, Johnston J, Macdonald A, White R, Powlson D (2018) Major limitations to achieving “4 per 1000” increases in soil organic carbon stock in temperate regions: evidence from long-term experiments at Rothamsted Research, United Kingdom. *Global Change Biology* **24**, 2563–2584. doi:10.1111/gcb.14066
- Prout JM, Shepherd KD, McGrath SP, Kirk GJD, Haeefe SM (2021) What is a good level of soil organic matter? An index based on organic carbon to clay ratio. *European Journal of Soil Science* **72**, 2493–2503. doi:10.1111/ejss.13012
- Purvis B, Mao Y, Robinson D (2019) Three pillars of sustainability: in search of conceptual origins. *Sustainability Science* **14**, 681–695. doi:10.1007/s11625-018-0627-5
- Rutter SM (2010) Review: grazing preferences in sheep and cattle: Implications for production, the environment and animal welfare. *Canadian Journal of Animal Science* **90**, 285–293. doi:10.4141/cjas09119
- Shepley E, Bergeron R, Bécotte F, Vasseur E (2017a) Dairy cow preference for outdoor access during winter under Eastern Canada climatic conditions. *Canadian Journal of Animal Science* **97**, 1–5. doi:10.1139/cjas-2016-0028
- Shepley E, Bergeron R, Vasseur E (2017b) Daytime summer access to pasture vs. free-stall barn in dairy cows with year-long outdoor experience: a case study. *Applied Animal Behaviour Science* **192**, 10–14. doi:10.1016/j.applanim.2016.11.003
- Shortall O (2019) Cows eat grass, don’t they? Contrasting sociotechnical imaginaries of the role of grazing in the UK and Irish dairy sectors. *Journal of Rural Studies* **72**, 45–57. doi:10.1016/j.jrurstud.2019.10.004
- Sjöström K, Fall N, Blanco-Penedo I, Duval JE, Krieger M, Emanuelson U (2018) Lameness prevalence and risk factors in organic dairy herds in four European countries. *Livestock Science* **208**, 44–50. doi:10.1016/j.livsci.2017.12.009
- Smid A-MC, Weary DM, von Keyserlingk MAG (2020) The influence of different types of outdoor access on dairy cattle behavior. *Frontiers in Veterinary Science* **7**, 24. doi:10.3389/fvets.2020.00257
- Smith J, Leach K, Rinne M, Kuoppala K, Padel S (2012) Integrating willow-based bioenergy and organic dairy production-the role of tree fodder for feed supplementation. *Agriculture and Forestry Research* **362**, 394–397. http://orgprints.org/21758/1/Smith_20AHCproceedings_2012.pdf.
- Stafford KJ, Gregory NG (2008) Implications of intensification of pastoral animal production on animal welfare. *New Zealand Veterinary Journal* **56**, 274–280. doi:10.1080/00480169.2008.36847
- Thompson R (2009) Sustainability of hill sheep flocks in England. *Small Ruminant Research* **86**, 71–73. doi:10.1016/j.smallrumres.2009.09.021
- Vaarst M, Alban L, Mogensen L, Milan S, Thamsborg , Kristensen ES (2001) Health and welfare in Danish dairy cattle in the transition to organic production: problems, priorities and perspectives. *Journal of Agricultural and Environmental Ethics* **14**, 367–390. doi:10.1023/A:1013060304868
- Vasconcelos E (2019) Le programme “Leite de Vacas Felizes” aux Açores: un levier du bien-être des vaches au pâturage. *Fourrages* **239**, 247–251.
- Vieira FMC, Deniz M, Vismara ES, Herbut P, Pilatti JA, Sponchiado MZ, de Oliveira Poretz B (2020) Thermoregulatory and behaviour responses of dairy heifers raised on a silvopastoral system in a subtropical climate. *Annals of Animal Science* **20**, 613–627. doi:10.2478/aoas-2019-0074
- von Keyserlingk MAG, Rushen J, de Passillé AM, Weary DM (2009) Invited review: the welfare of dairy cattle-key concepts and the role of science. *Journal of Dairy Science* **92**, 4101–4111. doi:10.3168/jds.2009-2326
- Wagner K, Brinkmann J, March S, Hinterstößer P, Warnecke S, Schüller M, Paulsen HM (2018) Impact of daily grazing time on dairy cow welfare-results of the welfare quality[®] protocol. *Animals* **8**, 1. doi:10.3390/ani8010001
- Wilkinson JM, Lee MRF (2018) Review: use of human-edible animal feeds by ruminant livestock. *Animal* **12**, 1735–1743. doi:10.1017/S175173111700218X
- Wilkinson JM, Lee MRF, Rivero MJ, Chamberlain AT (2020) Some challenges and opportunities for grazing dairy cows on temperate pastures. *Grass and Forage Science* **75**, 1–17. doi:10.1111/gfs.12458

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