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A biological integrity framework for describing animal welfare and wellbeing

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ABSTRACT

Ethical treatment of animals is the keystone of livestock production. Assessment of welfare is integral to assurance that animals experience a good life. Underpinning assurance are concepts of what constitutes good welfare, a good life and wellbeing. This review examines the concepts of welfare and wellbeing and the frameworks that have been developed for describing their scope. Historically, the tripartite model of welfare (feeling well, functioning well, leading a natural life) has been translated into the Five Freedoms (FF), Five Domains (FD), Good Life (GL), Welfare through Competence (WtC) and OIE World Organisation for Animal Health Welfare Principles frameworks. These frameworks provide scaffolds for numerous welfare assessment schemes. However, the three-part model of wellbeing (eudaimonia, hedonia, social interaction) lacks an explicit assessment framework, although FD, GL and WtC implicitly address aspects of wellbeing. Whereas positive affective (hedonic) experiences are considered to constitute positive welfare, positive aspects of eudaimonic function and social interaction are considered to be aspects of wellbeing above and beyond any indirect contribution they make to positive affective experiences (i.e. positive welfare). In this view, positive health is more than the absence of ill-health and positive social interactions are more than freedom from social isolation. New phenotypes in farm animals identified through analysis of sensor data are providing new perspectives on the functional integrity of biological processes that align well with concepts of wellbeing. These analyses draw on methods in resilience theory to examine stability in complex dynamic systems, specifically, uniformity of trajectories, periodicity of biorhythms and complexity of networks. A framework is proposed that loosely partitions FF, FD, GL and WtC into inputs, opportunities, and outcomes. The framework positions the outcome of biological integrity within the context of input constraints that can generate harms and deficiencies, and environmental opportunities that can foster acquisition of competencies and flourishing. It combines the eudaimonic, hedonic and social aspects of wellbeing within the tripartite terminology of welfare. It is hoped that the framework can help orientate new descriptions of biological function in farm animals derived from sensor data within the broader literature on welfare and wellbeing.

Keywords: behavioural complexity, biorhythms, competence, eudaimonia, hedonia, idiographic, positive biology, positive health, positive welfare, precision welfare assessment, resilience, robustness, sensors, welfare, wellbeing.

Introduction

The assessment of farm animal welfare underpins determination of regulatory compliance, assurance for product marketing, and comparison of performance between livestock enterprises in welfare benchmarking schemes. In addition, measurements made during welfare assessments are increasingly being used to describe phenotypes for genetic evaluation and breeding. The evolution of assessment protocols has involved on-going dialogue about what constitutes animal welfare. Stafleu *et al.* (1996) suggested that discussion of animal welfare occurs with varying degrees of abstraction, which they described as conceptual, explanatory and operational levels of description. The dialogue includes development of conceptual constructs of welfare, and explanation of the constructs through frameworks that attempt to describe the scope of the concepts. This explanatory step can include population of frameworks with input and outcome criteria that encompass aspects of (1) the animals' environment, including management practices, and (2) the animals' biological functions, which together influence their individual subjective experiences. Finally, the frameworks are operationalised by development of detailed measurement protocols to assess the welfare status of the animals under review (Stafleu *et al.* 1996; Bracke *et al.* 1999*a*). Included in this dialogue has been examination of the concept of wellbeing. Wellbeing is a term that is widely used in the health, welfare, production and animal breeding literatures and this usage draws attention to a need to reconsider the relationships between welfare and wellbeing. In this paper, I give an overview of the concepts of animal welfare and animal wellbeing, and how these have been explained through the frameworks known as Five Freedoms, Five Domains, Good Life, Welfare through Competence and OIE World Organisation for Animal Health Welfare Principles. From that background, a proposal is made that integrates aspects of these earlier frameworks for the purposes of articulating the concepts of welfare and wellbeing through a single explanatory framework.

The concept of animal welfare

A systematic approach to describing what animal welfare is and how it can be measured commenced in the UK in the 1960s, in response to public concern over 'factory farming'. The report of Brambell (1965, p. 9) into the welfare of intensively housed livestock concluded that 'Welfare is a wide term that embraces both the physical and mental wellbeing of the animal. Any attempt to evaluate welfare, therefore, must take into account the scientific evidence available concerning the feelings of animals that can be derived from their structure and functions and also from their behaviour.' The committee recommended that 'an animal should at least have sufficient freedom of movement to be able without difficulty, to turn round, groom itself, get up, lie down and stretch its limbs' (p. 13). The recommendation became known as the Five Freedoms and was subsequently refined by UK Farm Animal Welfare Council (FAWC) to include Provisions as to how Freedoms might be met (Webster 2016). FAWC (2009*a*) described the Five Freedoms and Provisions as follows:

- Freedom from hunger and thirst – by ready access to fresh water and a diet to maintain full health and vigour
- Freedom from discomfort – by providing an appropriate environment, including shelter and a comfortable resting area
- Freedom from pain, injury and disease – by prevention or rapid diagnosis and treatment
- Freedom to express normal behaviour – by providing sufficient space, proper facilities and company of the animal's own kind
- Freedom from fear and distress – by ensuring conditions and treatment that avoid mental suffering

Mellor and colleagues (Mellor and Reid 1994; Mellor and Beausoleil 2015; Mellor 2017) adapted the Five Freedoms to develop a framework based on Five Domains for describing the scope of physical and mental activities that encompass an animal's welfare. The Five Domains model provides a stronger focus on mental experiences than does the Five Freedoms model by viewing positive and negative occurrences in four physical/functional domains (Nutrition, Health, Environment, Behaviour) as inputs that generate the fifth domain (Mental experience), which, in turn, represents an integrated welfare outcome (Webster 2016; Johnson *et al.* 2022). Coe (2017) and Webber *et al.* (2022) reframed the Five Freedoms to describe positive welfare in zoo animals, as follows:

- Freedom to achieve competence – through effective performance of normal functions
- Freedom to have choice – through the right or ability to choose
- Freedom to take control – through the power to influence . . . the course of events
- Freedom to experience variety – through the quality of being different or diverse; the absence of uniformity or monotony.
- Freedom to engage complexity – through the quality of being intricate or complex

Refinement of the summary wording and the technical details of these frameworks is ongoing and occurs in combination with continuing debate on what constitutes good welfare and positive welfare. Fraser (1999, p. 178, italics in original) suggested 'that animals should *feel well* by being free from prolonged or intense fear, pain and other unpleasant states, and by experiencing normal pleasures; that animals should *function well* in the sense of satisfactory health, growth and normal behavioural and physiological functioning; and that animals should *lead natural lives* through the development and use of their natural adaptations'. Broom (1986, p. 524) provided a synopsis of welfare as 'the state of the animal as regards its attempts to cope with its environment'. Hurnik (1988, p. 107) captured the importance of the animal and the environment as an interdependent unit by suggesting 'Animal wellbeing is a state or condition of physical and psychological harmony between the organism and its surroundings.'. More recently, Dawkins (2008, p. 937; 2021*a*, p. 11) suggested that welfare is 'health and what animals want'. The importance of the individual animal's subjective experience in shaping its welfare was captured by Webster (2013, p. 3) in the following terms: 'The welfare of any sentient farmed animal ... is defined by its individual perception of its own physical and emotional state.'. Similarly, Bracke *et al.* (1999*a*, p. 282) suggested that welfare is 'determined by all the emotional states and only the emotional states in so far as they are experienced subjectively by that animal'. The OIE World Organisation for Animal Health (OIE 2021, Article 7.1.1) has drawn these concepts together to say 'animal welfare means the physical and mental state of the animal in relation to the conditions in which it lives and dies. An animal experiences good welfare if the animal is healthy, comfortable, well nourished, safe, is not suffering from unpleasant states such as pain, fear and distress, and is able to express behaviours that are important for its physical and mental state'. Fraser (2008) consolidated the description of welfare into a tripartite model in which welfare entails biological functioning, mental (affective) states, and natural living (Fig. 1). It is considered necessary for each of these aspects of the animal's life to be fulfilled for the animal to be in a state of good welfare (Fraser 2008). Nonetheless, the aspects are not considered to be entirely independent; mental (affective) experiences are recognised to be part of biological functioning, and *vice versa* (Hemsworth *et al.* 2015). However, healthy biological functioning does not guarantee positively valenced affective experience, and *vice versa* (Webster 2016; Williams 2021). For example, an aging cow may experience positive affective experiences from suckling and grooming her calf yet be in a poor physical state due to seasonal conditions and the debilities of advancing age. For further discussion of welfare as a subjective versus objective state of the animal see Bracke *et al.* (1999*a*) and Verhoog (2000).

What is wellbeing?

The concept of animal welfare draws much of its heritage from biology (Fraser *et al.* 2013). Wellbeing, in contrast, draws its heritage from philosophy. From at least the time of the ancient Greek philosophers, humans have wondered what it means to have 'a good life' (Appleby and Sandøe 2002; Nordenfelt 2006; Ryff *et al.* 2021). Continuing from these early writings to the present day, two prominent aspects of a good life are described as eudaimonia and hedonia. Eudaimonia describes the capacity of the human or animal to express agency, function well, fulfil biological potential and express mastery over its environment (Nordenfelt 2011; Ryff *et al.* 2021; Williams 2021). This contrasts with hedonia, which describes pleasant (positively valenced affective) mental experiences (Ryff *et al.* 2021; Williams 2021). Social interactions (also described as connectedness) are often included within the concept of eudaimonia (Ryff *et al.* 2021), although sometimes they are described as a separate third aspect of wellbeing (Fig. 1; Williams 2021). These three aspects of wellbeing can be summarised as 'doing', 'feeling' and 'interacting' (Fig. 2; Lawrence *et al.* 2019; Colditz 2022).

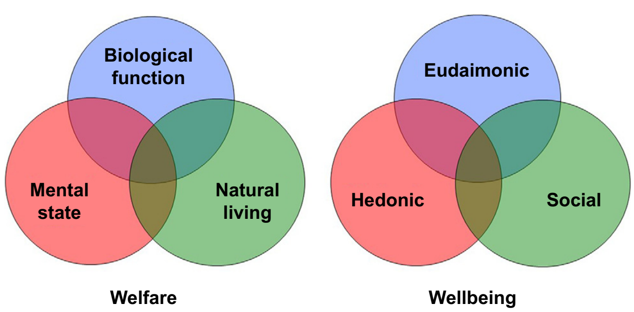

Fig. 1. Welfare is described by a tripartite model with aspects of biological functioning, natural living and mental state. Wellbeing is described as combining eudaimonic, hedonic and social aspects. Strong similarities exist between the two models.

An alternative parsing describes three aspects of human and animal wellbeing as perfectionism, desire fulfilment and hedonism (Appleby and Sandøe 2002). In this construction, perfectionism describes the fulfilment of an objective list of biological functions, whereas desire fulfilment and hedonism are two aspects of the subjective mental experience of feelings. A materialist view of biology understands preferences and hedonic experiences to be grounded in (neuro-) physiological and behavioural activities, and to serve a functional role in the fulfilment of the biological potential of the animal (Budaev *et al.* 2020), a view termed hedonic perfectionism (Appleby and Sandøe 2002). Nonetheless, whereas feelings emerge as a system property of (neuro-) physiological and behavioural activities, they have a subjective quality that cannot be reduced to the mere description of the constituent physical activities (Verhoog 2000; Mendl *et al.* 2010; Budaev *et al.* 2020). As a consequence, from a philosophical perspective, the feelings that attend desire fulfilment and hedonism are attributed a subjective value for the animal as an aspect of its wellbeing that is not adequately captured by current measures of physical functioning. Perfectionism and eudaimonia align closely with physical function and natural living in the tripartite model of animal welfare (Fig. 1). An outline of the relationships between the concepts addressed by animal welfare and wellbeing is presented in Fig. 3.

Three additional accounts of welfare and wellbeing are important to note. Rowland *et al.* (2021) proposed applying network theory to describe welfare as the state that arises through the interactions between various biological functions in the animal. Budaev *et al.* (2020) developed a computational model of wellbeing grounded in the account of biological function termed active inference that has prominence in the neurosciences. This account describes biological functions as an ensemble of processes through which the organism reconciles discrepancies between its expectations and current experience by acting on its environment and by

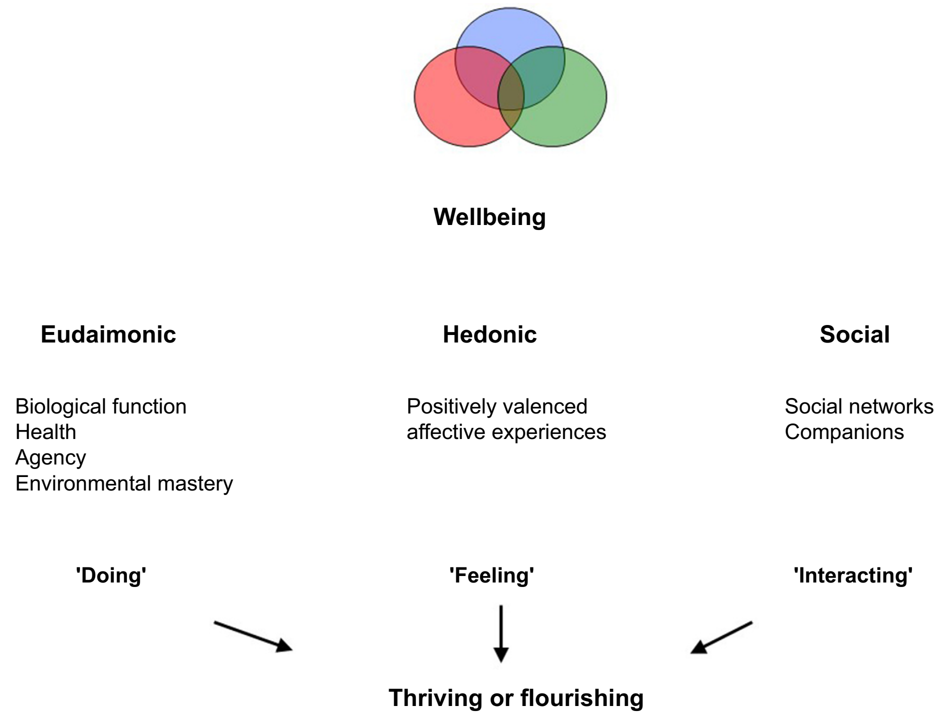

Fig. 2. In the three-factor model of wellbeing, eudaimonic, hedonic and social wellbeing combine in the positive outcome of thriving or flourishing.

updating its expectations (Colditz 2018, 2020; Kristiansen and Fernö 2020). This pattern of biological activity is continuously re-iterated over timescales that span intervals from moments to generations, and generates an outcome with equivalence to the process of approximate Bayesian inference. Wellbeing in this model is the subjective perception of discordance between expectation and sensory experience (Budaev *et al.* 2020). The account formalises a longstanding view that behavioural and physiological activities serve to harmonise the animal with its environment by reducing discrepancies and maintaining homeostasis (e.g. Stafleu *et al.* 1996; Bracke *et al.* 1999*b*).

These two accounts highlight the influence of models of biological function on the concept of what constitutes welfare and wellbeing. The third account of note is grounded in the model of physiological and behavioural regulation as a process of allostasis (Sterling 2012). From this perspective, Korte *et al.* (2007, p. 427) stated that 'Good animal welfare is characterised by a broad predictive physiological and behavioural capacity to anticipate environmental challenges' that ensures good welfare is achieved 'when the regulatory range of allostatic mechanisms matches the environmental demands.'. This model of welfare as a state of adaptive synchronisation of internal needs with external resources through anticipation and dynamic adjustment of physiological and behavioural activities is a core element of the computational model developed by Budaev *et al.* (2020) and the Bayesian model of biological function described above (Kristiansen and Fernö 2020).

In early discussions of the concept of animal welfare, it was often considered that for practical purposes, welfare and wellbeing could be considered synonymous (e.g. Duncan and Dawkins 1983; Mellor and Reid 1994). When a distinction was drawn, the difference was usually seen to lie in the scope of animal experience addressed by the two concepts. Welfare, it was suggested, covers the full spectrum from bad to good experience, whereas the focus of wellbeing is on the positive experiences of the animal's life that enable it to thrive and flourish (Yeates and Main 2008; Webster 2021; Williams 2021; Colditz 2022). Webster (2021, p. 8) described the distinction in the following terms: 'Welfare describes the physical and mental state of an animal across the whole spectrum from very good to very bad. Wellbeing describes a state within the range of satisfactory to good and must therefore be the aim of good husbandry.'. Wellbeing is a term in wide usage in animal science and animal breeding where it appears to describe an integrated whole-of-animal condition often embracing the whole of the animal's life. This broad-brush usage may be in part to distance the terminology from studies that undertake a more focused examination of individual components of welfare. The pragmatic approach adopted here is to draw insights from the philosophical and biological heritages of both concepts. The most important shared insight is the concept that animals can attain 'positive' states. The study of positive states has been termed positive biology.

<table>
<tr><th colspan="2" rowspan="3">Animal welfare
(following Fraser 1999)</th><th colspan="4">Wellbeing</th></tr>
<tr><th>Humans</th><th>Animals</th><th colspan="2" rowspan="2">Alternative model
(following Williams 2021)</th></tr>
<tr><th colspan="2">(following Appleby and Sandøe 2002)</th></tr>
<tr><td rowspan="3">Feel well</td><td rowspan="3">Free from prolonged or intense fear, pain and other unpleasant states, and by experiencing normal pleasures</td><td rowspan="2">Hedonism</td><td>Pleasure, suffering</td><td rowspan="2">Hedonia
(feeling)</td><td>Positive affect</td></tr>
<tr><td rowspan="2">Preferences</td><td rowspan="2">Positive social function</td></tr>
<tr><td rowspan="2">Desire fulfilment</td><td rowspan="2">Social wellbeing
(interacting)</td></tr>
<tr><td rowspan="2">Lead natural lives</td><td rowspan="2">Development and use of natural adaptations</td><td rowspan="3">Natural living</td><td rowspan="4">Fulfilling inherited and develop-mentally acquired potential</td></tr>
<tr><td rowspan="5">Perfectionism</td><td rowspan="5">Eudaimonia
(doing)</td></tr>
<tr><td rowspan="4">Function well</td><td rowspan="4">Satisfactory health, growth and normal behavioural and physiological functioning</td></tr>
<tr><td rowspan="3">Fulfilling functional potentials</td></tr>
<tr><td>Environmental mastery</td></tr>
<tr><td>Agency</td></tr>
</table>

Fig. 3. A map of the relationships between concepts addressed by animal welfare and wellbeing.

What is positive biology?

The initial focus of assessing welfare and improving husbandry was on minimising exposure of animals to harms and deprivations (Broom 1986). Any harm can compromise wellbeing, while none is individually necessary for an animal to be in a state of poor welfare (see fig. 2 in Colditz 2022). It was recognised that above and beyond the absence of harms and deprivations, animals could have experiences that promote (1) positive mental states, (2) the development of capabilities (competencies) to cope with their environment, (3) positive health and (4) a thriving physiological status (Ryff *et al.* 2004; Boissy *et al.* 2007; Yeates and Main 2008; Yeates 2011; Colditz and Hine 2016; Mellor 2016; Coe 2017; Lawrence *et al.* 2019; Beck and Gregorini 2020; Rault *et al.* 2020; Williams 2021; Colditz 2022; Düpjan and Dawkins 2022; Webber *et al.* 2022). These positive experiences have been drawn together in the concepts of 'quality of life' (Vigors *et al.* 2021; Reid *et al.* 2022), a 'life worth living' (Yeates 2011; Mellor 2016; Webster 2016) and a 'good life' (FAWC 2009*b*; Edgar *et al.* 2013; Rowe and Mullan 2022). In the welfare tradition, positive aspects are described as pleasant mental (i.e. positively valenced hedonic) experiences (Boissy *et al.* 2007; Yeates and Main 2008; Mellor 2015; Düpjan and Dawkins 2022). The concept of wellbeing makes an important contribution by recognising that eudaimonic biological functioning, environmental mastery and social connectedness are also important (non-hedonic) aspects of positive experience (Deci and Ryan 2008; Beck and Gregorini 2020; Rault *et al.* 2020; Ryff *et al.* 2021; Williams 2021; Colditz 2022) rather than merely providing indicators of the absence of harms. The concept of wellbeing helps parse the positive outcomes recognised in the Good Life, Welfare through Competence and Five Domains frameworks into hedonic and non-hedonic benefits. As summarised by Fraser's (2008) tripartite model, positive welfare/wellbeing is not encompassed by a single physical function or mental state of the animal. In contrast to harms where any harm is sufficient to compromise welfare/wellbeing; for the animal to experience positive welfare/wellbeing it needs to express a suite of physical functions and mental experiences, all of which may be necessary and none of which may be alone sufficient to deliver a positive state (Fraser 2008). This account of wellbeing accords with the definition of health in the constitution of the World Health Organization (WHO 1946) as 'a state of complete physical, mental and social wellbeing and not merely the absence of disease or infirmity'. It is important to note the counter view that welfare and wellbeing are subjectively experienced by the animal solely as its emotional state (e.g. Bracke *et al.* 1999*a*, 1999*b*; Budaev *et al.* 2020).

Historically, the primary focus of health studies has been on the causes of harms and deficits, with a view to the design of interventions and remedies to prevent and control diseases and functional disorders. Notwithstanding this focus on negatives, there is also a long tradition of studies on the role of environmental cues and experiences during prenatal and postnatal life in shaping the developmental trajectories of traits and the acquisition of morphological, physiological, immunological, behavioural and psychological competencies and capabilities. These two research streams have recently been termed negative and positive biology (Farrelly 2012). Experiences and environmental cues, especially during sensitive periods of development, can have long-lasting consequences through epigenetic and behavioural conditioning that can equip the animal with a capacity to cope with short-term environmental disturbances and to adapt to longer-term environmental conditions (Boissy *et al.* 2007; Colditz and Hine 2016; Colditz 2018; Capitanio and Mason 2019; Lyons and Schatzberg 2020; Parois *et al.* 2022*a*, 2022*b*). Heritable factors also contribute to these positive outcomes (Berghof *et al.* 2019*a*). Many decades of research, which is too numerous to list here, provides evidence of the contribution of environmental conditions to the strength of immune function, gut health, expression of agency, social competence and mastery over environmental challenges. Within studies on positive biology, the instructive role of mild negative episodes is recognised as contributing to positive outcomes, as seen, for example, in low-stress stock-handling methods (Grandin 2004), a point Ryff (2022) noted that is often overlooked in human positive psychology, but is now being acknowledged in its so-called second wave (Lomas 2016). The importance of positives is captured by the observations that positive health is more than the absence of ill-health (Ayres 2020) and that social wellbeing is more than freedom from social isolation (Pomerantz and Capitanio 2021), as recognised by WHO (1946). Thus, positive biology is more than a semantic distinction between 'good' and 'positive' to be the study of processes lying outside the domain of 'host defence mechanisms' that equip the animal with a capacity to flourish. For further discussion of positive health, see Colditz (2022). For reviews on physiological, health and behavioural indicators of eudaimonic wellbeing, see reviews by Ryff *et al.* (2004, 2021), Williams (2021) and Düpjan and Dawkins (2022). For a review of the role of positive developmental experiences in enabling positive emotional outcomes in later life, see Boissy *et al.* (2007).

Frameworks for assessment

The translation of the concepts of welfare, wellbeing and a good life into explanatory instruments for assessment of the physical and mental state of the animal has been guided by several frameworks, namely, Five Freedoms, Five Domains, Good Life, Welfare through Competence, and OIE Welfare Principles. Some of the similarities and differences among the frameworks are summarised in Fig. 4. Webster (2016) suggested that the Five Freedoms framework provides a simple and timeless guide to right action through a focus on outcomes. However, he went on to say that it does not attempt to provide a complete picture of the mental state or welfare of the animal. In contrast, the Five Domains provide a more detailed framework for assessing individual and combined effects of the physical, social and management environment on mental outcomes for the animal that, it has been suggested, is more readily amenable to amendment in light of new knowledge about biological processes and outcomes. The Five Domains, Webster (2016) suggested, have utility for designing and testing the impact of practices on welfare as illustrated for piglets by Johnson *et al.* (2022). The Five Domains framework addresses the impacts on the welfare of the animal of both negative and positive experiences, and the need for provision of environmental conditions that nurture positive mental experiences. Thus, the Five Domains model has a stronger focus on positive biology than does the Five Freedoms model. The Good Life framework moves on from assessment of negatives to focus on provision of the resources needed for the animal to have opportunities to attain a good life (Edgar *et al.* 2013; Rowe and Mullan 2022). Similar to the Good Life framework are the five 'Opportunities to Thrive' described for wildlife kept in captivity as (1) opportunity for a thoughtfully presented, well balanced diet, (2) opportunity to self-maintain, (3) opportunity for optimal health, (4) opportunity to express species-specific behaviour, and (5) opportunity for choice and control (Miller *et al.* 2020). In the Welfare through Competence framework, opportunities for achieving competence are enabled by environments that provide choice, control, variety, and complexity (Webber *et al.* 2022). OIE Welfare Principles draw on the Five Freedoms to provide a globally applicable framework for the development of international standards that emphasise animal-based outcomes as measures of welfare (OIE 2021). Stronger emphasis is placed on minimisation of harms than on attainment of positives. The OIE Code (Article 7.1.3) notes: 'Some measures of animal welfare involve assessing the degree of impaired functioning associated with injury, disease and malnutrition. Other measures provide information on animals' needs and affective states such as hunger, pain and fear, often by measuring the strength of animals' preferences, motivations and aversions. Others assess the physiological, behavioural and immunological changes or effects that animals show in response to various challenges.'. A further framework

Five Freedoms		Five Domains		Good Life		Welfare through Competence		OIE Welfare
Principles	Provisions	Principles	Provisions	Principles	Provisions	Principles	Provisions	Principles
Freedom from thirst, hunger and malnutrition	By providing ready access to fresh water and a diet to maintain full health and vigour	Nutrition	Water			Nutrition	Competence described as physical, mental, innate, and learned functional abilities to realise desired outcomes effectively and efficiently is achieved through provision within each domain of opportunities enabling choice, control, variety, and complexity	Access to sufficient feed and water, suited to age and needs, to maintain health and productivity and prevent prolonged hunger, thirst, malnutrition or dehydration.
			Food					
Freedom from discomfort and exposure	By providing an appropriate environment including shelter and a comfortable resting area	Environment	Comfort	Comfort	Comfortable physical environment	Environment		Physical environment to allow safe and comfortable resting, moving, postural changes and opportunity to perform motivated natural behaviours.
			Physical features		Comfortable thermal environment			Air quality, temperature and humidity to support good animal health and natural methods of thermo-regulation.
					Safe environment			Physical environment suited to the species to minimise injury and disease transmission
Freedom from pain, injury, and disease	By prevention or rapid diagnosis and treatment	Health	Disease	Healthy life	Management policy for positive health	Physical Health		Animals suited to the local climate and able to adapt to local diseases, parasites and nutrition.
								Diseases and parasites prevented and controlled through good management. Isolated, treated promptly or killed humanely if necessary serious health problems.
			Injury					Pain managed for necessary painful procedures
					Breeding for positive welfare			Health and welfare included in breeding objectives.
			Function		Promoting a natural body type (telos)			Animals suited to the local climate and able to adapt to local diseases, parasites and nutrition.
Freedom from fear and distress	By ensuring conditions and treatment which avoid mental suffering	Mental State	Emotions	Interest	Enriched environment	Behavioural interaction		Handling should foster a positive relationship with humans and not cause injury, panic, lasting fear or avoidable stress.
			Agency		Enhanced learning opportunities			
			Pleasures	Confidence	Positive experiences with people			
Freedom to express normal behaviour	By providing sufficient space, proper facilities and company of the animal's own kind	Behaviour	Behaviour rewards		Positive social interactions			Social grouping to allow positive social behaviour and minimise injury, distress and chronic fear.
				Pleasure	Food enrichment			
			Behaviour expressions		Play opportunities			Physical environment suited to the species to minimise injury and disease transmission
					Breeding and nurturing opportunities			

Fig. 4. Summary of the Principles and enabling Provisions for the Five Freedoms, Five Domains, Good Life, Welfare through Competence, and OIE Welfare Principles frameworks. An approximate alignment of concepts across the frameworks is presented.

for explaining the concept of welfare is important to note. The Vienna Framework has been developed to assist scientists clarify whether their research on positive welfare addresses 'hedonic positive welfare' or 'positive welfare balance' (Rault *et al.* 2020). The authors note the potential contribution of eudaimonia to positive welfare without incorporating it within the Vienna Framework.

In addition to these frameworks, Bracke *et al.* (1999*a*, 1999*b*, 1999*c*) described a method of semantic modelling for developing a framework for welfare assessment. The method uses scientific statements from published literature and expert opinion to identify and weigh indicators of welfare on the basis of expert biological knowledge of animal needs, and has been applied in the development of the Salmon Welfare Index Model (SWIM, Stien *et al.* 2013; Pettersen *et al.* 2014).

Measurement and interpretation of animal-based outcomes

The frameworks provided by the Five Freedoms, Five Domains, Good Life, Welfare through Competence, and OIE Welfare Principles have guided the development of criteria and detailed protocols for checking and quantifying inputs and animal-based outcomes to enable assessment of welfare and wellbeing. These frameworks can be described as 'compartment' models in that they divide biological functions into categories described as freedoms, domains, needs, etc. (Fig. 5). The compartments are grounded in mechanistic models of how animals work, for example, by fulfilling needs (e.g. satisfying hunger) and expressing biological activities (e.g. growth; Bracke *et al.* 1999*a*, 1999*b*). Assessment of welfare is then undertaken by measurement of inputs and outcomes relevant to each compartment. In the compartment approach to assessment, the detection of positive outcomes has been problematic (Miller *et al.* 2020; Keeling *et al.* 2021). In view of the importance of positive outcomes to the concepts of positive welfare and wellbeing, I will focus next on an alternative strategy for assessment of positives through a whole-of-animal approach that examines the 'structural' integrity of biological processes rather than assessment of specific functions within compartments.

The structural approach draws on methods in resilience theory for examining the stability of complex dynamic

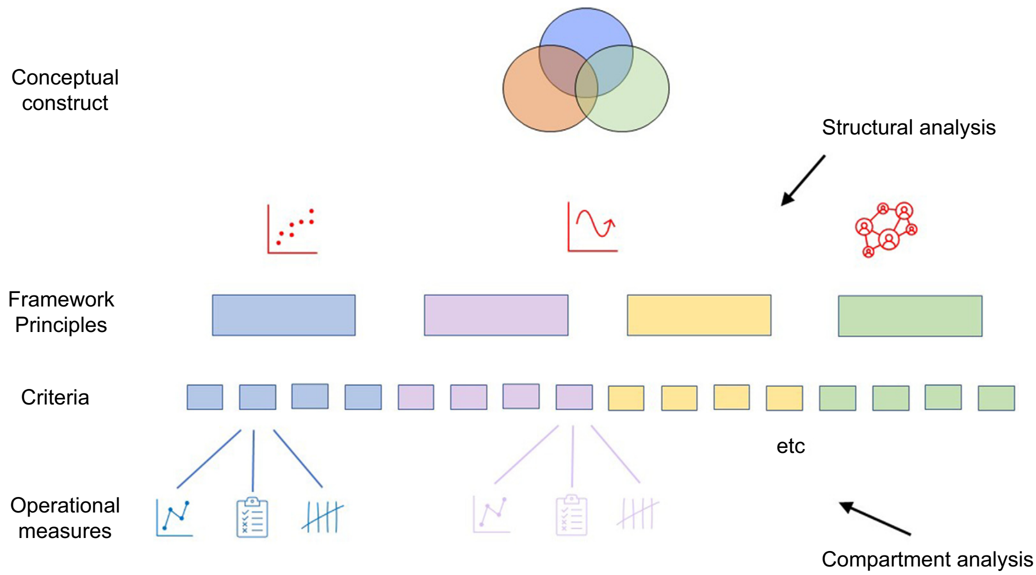

Fig. 5. Animal welfare can be described at conceptual, explanatory and operational levels. In a top-down approach, a conceptual construct of welfare or wellbeing is explained through a framework that contains compartments or categories (also described as Principles) such as Good Feeding, Good Housing, Good Health and Appropriate Behaviour as in WelfareQuality® (Botreau *et al.* 2007). These Principles can be further divided to delineate Welfare Criteria. An assessment scheme is composed of a suite of operational measurements, for example, covering input resources, management practices and animal outcomes, within each compartment described here as 'compartment analysis'. An alternative assessment strategy is to undertake structural analysis of biological functions that provide integrated measures of the systemic functional integrity of the animal described here as 'structural analysis'. In a bottom-up approach, new measurement technologies (for example, structural analysis of biological functions captured via sensor technologies) can show new aspects of biological function that inform and help refine the conceptual model of welfare or wellbeing.

systems (Scheffer *et al.* 2009, 2018). Three of the principal characteristics of stable systems are the *uniformity of trajectories* (Berghof *et al.* 2019*a*; Iung *et al.* 2020) such as growth rate and daily milk yield, *periodicity of biorhythms* (Scheibe *et al.* 1999; Wagner *et al.* 2021) such as body temperature and daily feeding activity, and *complexity of networks* (Asher *et al.* 2009; Miller *et al.* 2020; Heino *et al.* 2021) such as social interactions. Deviations from these three patterns increase as the capacity of an animal to cope with day-to-day fluctuations in its environment decreases (Scheffer *et al.* 2018; Weinans *et al.* 2021). Statistical methods for analysing the dynamic stability of these three characteristics of biological systems have been developed and validated in large datasets in dairy cows (Elgersma *et al.* 2018; van Dixhoorn *et al.* 2018; Adriaens *et al.* 2020; Poppe *et al.* 2020, 2021*a*, 2021*b*; Friggens *et al.* 2021; Sun *et al.* 2021), pigs (Putz *et al.* 2019; Revilla *et al.* 2019), chickens (Berghof *et al.* 2019*b*; Bedere *et al.* 2022), sheep (Nunes Marsiglio Sarout *et al.* 2018) goats (Mengistu *et al.* 2017; ben Abdelkrim *et al.* 2021) and fish (Mengistu *et al.* 2022). These studies draw on high-frequency records (e.g. daily milk yield) of individual animals acquired over extended periods of time (e.g. 305-day lactation). Many of these studies have found that stronger uniformity, periodicity and complexity indicate better current welfare and are predictive of better health outcomes and greater longevity.

The structural approach adopts the black box model (Knap and Doeschl-Wilson 2020), which is commonly applied in quantitative genetics, in which knowledge of underlying biological mechanisms is not a pre-requisite for measurement of traits and their subsequent application in breeding programs. Of course, knowledge of physiological and behavioural mechanisms and the contribution of genes to those mechanisms can improve description of traits and prediction of breeding values, and mechanistic research is a very strong focus of genetic studies (Mackay *et al.* 2009). When applied to animal welfare and wellbeing, the black box approach does not rely on knowledge of the activity of host response pathways to interpret the significance of changes in biological functions as indicators of welfare and wellbeing (Wagner *et al.* 2021). Once again, knowledge of underlying mechanisms can help with interpretation but is not necessary. Perhaps not surprisingly, the structural approach is being rapidly developed in phenotyping studies through statistical analysis of longitudinal data sets generated by sensor technologies.

Box 1. Example of analysis of biorhythms for the assessment of welfare in dairy cows

Wagner *et al.* (2021) described detection of welfare events from the analysis of behavioural activity data determined from individual animal locations within dairy barns. A variable called 'activity level' was estimated by applying pre-determined weights to the time an animal spent in various locations within the barn on the basis of communication between an animal-borne transponder and a base station once per second. Circadian patterns in behavioural activity level were then analysed. Data were sourced from historical records from four farms representing more than 120 000 cow × days. Several methods for analysis of times series data were explored. The authors settled on a method they termed 'Fourier-Based Approximation with Thresholding'. Abnormalities in the circadian pattern of behavioural activity level were validated against stockperson records of cow health, including accidents, lameness, oestrus, calving, mastitis, rumen acidosis, other diseases, mixing, other disturbances and inflammation caused by intramammary injection of bacterial endotoxin. The method detected abnormal rhythms associated with 95% of health and reproductive events. Rhythm abnormalities were detected up to 35 h before stockperson recording of the occurrence of events.

The study illustrates several important points.

(1) Disturbance in the circadian pattern of behavioural activity was highly sensitive for detecting compromised welfare and reproductive events such as oestrus and calving
(2) Disturbance in the circadian pattern of behavioural activity provided a generic prodromal indicator of impending compromised welfare that lacked diagnostic specificity for identifying the cause of disturbance. This is in accord with the description of 'structural' measures of biological function as providing holistic measures that represent the integrated biological function of the animal.
(3) Sensor data were not decomposed into basic behavioural activities such as resting, standing, walking, and eating for the purpose of subsequent interpretation within an ethological model of normal dairy cow behaviour. Thus, detection of disturbances did not rely on a normative model of behavioural activity with parameters such as resting time of 10–12 h per day, feeding time 2.5–7 h per day and so on.
(4) Detection of abnormalities was based on deviation from the prior circadian pattern in behavioural activity level expressed by each individual. Thus, the method provides individualised assessment of welfare, an approach termed idiographic analysis.
(5) Data extraction was tailored to the sensor system available to the researchers. While developmental work may be required for extraction and validation of an appropriate behavioural activity level variable from other sensor technologies (e.g. triaxial accelerometers), the underlying concept of biorhythm analysis should be applicable to other technologies for quantifying behavioural activity level (e.g. Nunes Marsiglio Sarout *et al.* 2018).
(6) Physiological variables such as body temperature may also be amendable to biorhythm analysis for detection of compromised welfare, as illustrated by the work of van Dixhoorn *et al.* (2018) and Sun *et al.* (2021).
(7) Structural analysis of biological functions for assessment of wellbeing needs to be combined with other methods when it is important to know the cause of a welfare-related event.
(8) Disturbance to circadian rhythm in behavioural activity level can provide a flag for the stock person to investigate the cause of the disturbance.
(9) Historical sensor datasets, when annotated with individual animal health and management data, can be used for development of methods for structural analysis of biological functions as an indicator of wellbeing.

Biorhythm analysis as an indicator of welfare is a topic attracting increasing attention. Other studies in sheep and cattle include Scheibe *et al.* (1999), Nunes Marsiglio Sarout *et al.* (2018), van Dixhoorn *et al.* (2018), Casey *et al.* (2022).

The analytical methods provide measures of the dynamic stability of the animal at a systemic level and can lack diagnostic specificity for identifying the nature and cause of deficits at the compartment level (Box 1; Wagner *et al.* 2021). In the terminology of disease diagnosis, change in the structure of biological functions is a 'prodrome' of developing dysfunction, which like most prodromes (e.g. fever), lacks diagnostic specificity for the cause of impending ill-health. In the terminology of resilience theory, these changes are described as 'early warning signals' of 'critical transitions' in system function (Scheffer *et al.* 2009, 2018) or 'dynamic indicators of resilience' (van Dixhoorn *et al.* 2018). A similar focus on identifying signs rather than causes of dysfunction is adopted in the Salmon Welfare Index Model 2.0 for assessing health as an indicator of welfare (Pettersen *et al.* 2014). In principle, appropriate variables could be chosen for structural analysis so that (dys)function could be determined at the level of individual compartments. Indeed, these variables could include indicators of positive affective (hedonic) experience (Dawkins 2021*b*). For example, structural analysis of 'affect dynamics' monitored via smart sensors is under intensive investigation in humans (e.g. Wampfler *et al.* 2022).

Most structural analyses rely on high-frequency records that can be analysed for short data runs such as a few days or for long data runs, such as a year or a whole lactation and can generate a single statistic for each animal for the period of evaluation that falls on a continuous scale. These analyses hold the potential to provide a much finer-grained indicator than can be achieved with most scoring systems employed in current compartment model schemes for welfare assessment (Knierim *et al.* 2021). As noted above, the measures usually lack diagnostic specificity for the causes of disturbance in function (Wagner *et al.* 2021). Nonetheless, system disturbances such as decreasing periodicity of biorhythms identified over short intervals such as a few days can flag the occurrence of events requiring investigation by a stockperson (Wagner *et al.* 2021).

Another important holistic measure of the integrity of biological function in wide use for welfare assessment is provided by qualitative behavioural assessment (Wemelsfelder *et al.* 2001). Through a process of free choice profiling, assessors choose terms to describe the global affective and physical state of the animal from observing its behaviour and demeanour. Like other holistic measures, qualitative behavioural assessment lacks diagnostic specificity to identify the causes of poor appearance.

Links between measures of functional integrity and resilience to stressors

Day-to-day fluctuations in system functions align with the timeframe for initiation and resolution of acute stress responses (Colditz and Hine 2016; Friggens *et al.* 2017). Evidence in support of a mechanistic link between daily variability in indicators of functional integrity and the dynamic stress status of the individual comes from several sources. In cows housed in barns, most of the day-to-day variation in milk yield is not synchronised across the group. Cows in a barn can be considered to have a shared environment but also to have a private non-shared environment, as shown for genetically identical mice housed as a single group (Freund *et al.* 2013). Asynchrony among cows in variation in milk yield suggests that individuals independently experience fluctuations in their non-shared environment. Whereas some of the stressors in the non-shared environment such as oestrus, mastitis, and lameness can be readily identified (Wagner *et al.* 2021), many remain unidentified (Garcia-Baccino *et al.* 2021). Cows with low resilience have many days on which their milk yield deviates from their individual lactation curve, whereas high-resilience cows exhibit fewer days with deviations. Occasionally, there is a disruption in the shared environment caused by an event such as a husbandry practice or change of feed. These shared 'stress' events are marked by a synchronised drop in milk yield in the whole herd. Poppe *et al.* (2021*b*) examined the association between high resilience and milk yield during stress events in the shared environment. Cows with high resilience had a lower drop in yield and returned more quickly to their individual milk yield trajectory than did low-resilience cows, analysed at the level of genetic correlations. The finding helps link responses observed to a stressor in the shared environment with individual variation associated within events in the non-shared environment. These findings have been extended by a study on energy partitioning in growing pigs. Lenoir *et al.* (2022) found a strong positive genetic correlation between variability in allocation of available energy to growth and variability in daily growth. Greater variability in the proportion of dietary energy allocated to growth suggests that pigs with low resilience were more frequently diverting energy to processes of defence and repair.

The effects of experimentally imposed stressors have been studied in pigs with developmentally acquired resilience. Responses to transport, heat exposure, immune challenge with bacterial endotoxin, a surgical skin wound, and social isolation were compared in pigs raised from birth in an enriched environment and conventionally raised pigs (Parois *et al.* 2022*a*, 2022*b*). 'Enriched' pigs exhibited faster physiological recovery from transport and endotoxin challenge and lower hair cortisol concentrations over the duration of the study period (Parois *et al.* 2022*a*). Enriched pigs had smaller increases in plasma cortisol, glucose and non-esterified fatty acids during transport, which is indicative of less mobilisation of energy reserves as a defence reaction to stress. In accord with these findings, during social isolation enriched pigs had lower heart rate, higher heart-rate variability, and higher vagal tone (Parois *et al.* 2022*b*). Across the study period, pigs from the enriched environment had lower variance in body weight than did conventionally raised pigs. In view of the prominent roles of cortisol and autonomic tone (indicated by heart rate and heart-rate variability) in modulating the moment-to-moment utilisation of energy (Mormède *et al.* 2011; Colditz 2021) and the occurrence of persistent variation among individuals in autonomic tone (Koolhaas *et al.* 1999; Koolhaas 2008; Colditz 2021), further studies on links among stress resilience, the dynamics of energy utilisation and uniformity of daily performance seem warranted. Together, these results suggest that uniformity of the growth trajectory that is interpreted as a resilience indicator in structural analyses is linked with an improved capacity to cope with a range of experimental stressors.

Notwithstanding the need for further mechanistic studies, it can be proposed that measures of the day-to-day integrity of biological systems are indicators of *positive* states to the extent that they describe integrated outcomes of activity within the underlying homeostatic networks that support the measured biological functions. Where studies on proximate mechanisms have shown an association of say, metabolite availability, immune function, infection, endocrine dynamics, stock person attitude, or affective state, etc. on biological activities such as milk yield or daily behavioural activity level, then it follows that structural integrity in these down-stream biological activities indicates that positive and negative inputs within the upstream regulatory networks are balanced in favour of a positive down-stream outcome.

In more general terms, the capacity to maintain integrity of biological functions in the face of short-term fluctuations in the shared and non-shared environments of the animal is an indicator of its resilience. Environmental change can also occur over longer timeframes. Persistent change in environmental conditions can trigger adaptation of the animal through longer-term structural, behavioural and metabolic changes that are indicators of its robustness (Knap 2005; Friggens *et al.* 2017). Hence, resilience describes the success of homeostatic processes in maintaining dynamic equilibrium from day-to-day and is usually assessed through analysis of *deviations* in biological processes. In contrast, robustness describes the success of the animal in adapting to different environments and is usually assessed through analysis of *means*, for example, as reaction norms (Knap 2005; Friggens *et al.* 2017; Knap and Doeschl-Wilson 2020).

Idiographic analysis of the state of the animal

Structural analyses usually rely on timeseries data for each animal within the group. An important consequence is the insight this provides on the individual's experience of its environment. The influence of the individual's perception of its own physical and mental state on its welfare (Bracke *et al.* 1999*a*; Webster 2013; Budaev *et al.* 2020) requires us to understand the individual's experience 'through its own eyes' (Dawkins 2006; Colditz 2018). A well recognised limitation of most assessment procedures is their reliance on snap-shot measures taken at infrequent intervals that generate cross-sectional data often on a subset of individuals within the group (Webster 2016; Keeling *et al.* 2021; Knierim *et al.* 2021). For cross-sectional data, the benchmark used to assess whether an individual is 'normal' is derived from normative statistics of the population (Veissier *et al.* 2011; Fisher *et al.* 2018; Haslbeck and Ryan 2022). Two important consequences are the potential for the average value for a 'normal' individual to be substantially different from the average of the 'normal' population, and for correlations among variables observed at the population level to not hold for the individual (Heino *et al.* 2021). Drawing incorrect inferences about individual behaviour from relationships observed at the group level is recognised as an 'ecological fallacy' that can lead to misleading or invalid conclusions (Fisher *et al.* 2018; Haslbeck and Ryan 2022). For example, a cortisol measure of an individual that falls more than 40% above the group mean has been suggested to indicate that the individual is stressed (Barnett and Hemsworth 1990). Yet, the genetic constitution of the individual may lead to its resting cortisol concentration being much higher than the group mean and an observed value more than 40% above the group mean may represent only a minor 'normal' deviation within the individual's own biology. The second problem, namely that correlations observed at the population level may not hold for the individual, can be illustrated with the example of estimated breeding values (EBVs) in livestock. Genetic correlations among traits observed at the population level are often not reflected in the EBV ranking of individuals for the correlated traits. An individual can have a high EBV for two traits that are negatively correlated at the population level. This divergence of the relationship between traits at the individual level helps enable favourable genetic progress at the population level in negatively correlated traits.

The estimation of the within-individual dynamics for measured variables is described as idiographic analysis. Structural analysis of within-individual dynamics in time-series data should help attain the goal of assessing the state of the individual through its own eyes (Dawkins 2006; Colditz 2018, 2022; Richter and Hintze 2019; Buller *et al.* 2020). Nonetheless, production animals such as fish and poultry that are often raised in very large populations will require innovative approaches for longitudinal monitoring of individuals to be possible (Torgerson-White and Sánchez-Suárez 2022).

A framework for integrated assessment of welfare and wellbeing

New information on variability in integrity of biological functions in production animals creates a need to orientate this knowledge within the landscape of welfare assessment. A framework is proposed for situating outcome indicators of biological integrity within the context of input constraints that can generate harms and deficiencies, and environmental opportunities that can foster acquisition of competences for flourishing (Fig. 6). The framework is grounded in the perspective from developmental biology that the phenotype of the animal and its moment-by-moment functions are conditioned by and emerge on a trajectory across the animal's life from interactions between its inherited and developmentally acquired potential and its contemporary environment (for reviews, see Boissy *et al.* 2007; Colditz 2022). Negatives addressed in other frameworks are identified in the proposed framework as input constraints that are broadly classified within categories of feed, environment, genotype, and management. Opportunities identified in the Good Life (Rowe and Mullan 2022) and Welfare through Competence (Webber *et al.* 2022) frameworks are incorporated as intermediaries lying between inputs and outcomes. Outcomes inspired by concepts in positive biology are broadly aligned within the tripartite model of welfare. The framework separates the

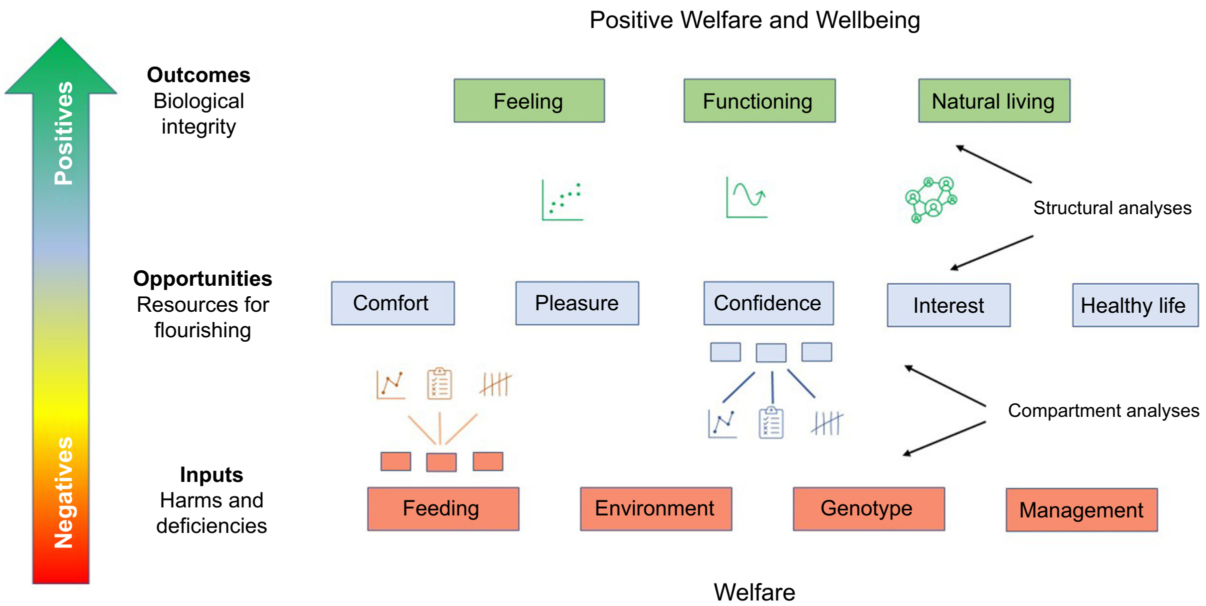

Fig. 6. A proposed framework for combining assessment of welfare and wellbeing. Inputs that can constrain and compromise welfare by causing harms and deficiencies include attributes of feeding, the environment, genotype, and management. Resources providing opportunities that can foster comfort, pleasure, confidence, interest, and a healthy life, as described in the Good Life framework, serve as intermediaries between inputs and positive outcomes. Positive outcomes associated with feeling, functioning and natural lives combine the focus of positive welfare on positive hedonic feelings, with the additional focus of wellbeing on eudaimonic and social wellbeing. Conventional assessment approaches grounded in reductionist diagnostic methodologies underpin compartment analyses to identify negative outcomes such as ill-health. Newer assessment approaches grounded in complex-systems science enable assessment of the integrity of functional outcomes both at the compartment level and at a more holistic level of integrated performance of the animal. Additional assessment methodologies such a Qualitative Behavioural Assessment (Wemelsfelder *et al.* 2001) can complement compartment and structural analyses. Criteria within compartments, as occurs in WelfareQuality® (Botreau *et al.* 2007), are shown for confidence and feeding. Use of the framework to guide development of assessment protocols would require its adaptation to address the species, production system and environment of interest.

negative and positive factors described within the Five Domains model into inputs that impose constraints and opportunities that foster flourishing (Fig. 6).

The framework proposed here incorporates the eudaimonic, hedonic and social aspects of wellbeing within the tripartite terminology of welfare, as suggested previously by Williams (2021). It combines the focus on positive (non-hedonic) benefits to wellbeing of physical function and social interactions, with the contemporary focus in positive welfare on positive affective states to create an integrated construct of positive welfare and wellbeing as illustrated in Fig. 6. It has been suggested that extending the concept of positive welfare beyond the facets of ‘hedonic positive welfare’ and ‘positive welfare balance’ risks diluting the concept (Rault *et al.* 2020). The counter proposition is made here that expanding the focus on positives within the animal’s life to include positive physical and social functions will strengthen appraisal of the animal’s state, broaden the biological foundations of positive welfare and wellbeing, and improve efforts to afford animals a life worth living. This view was expressed by Turner (2019, p. 367) in the following terms: ‘. . . if we are to take a holistic view of animal wellbeing, then positive animal welfare incorporates more than the net valence between positive or negative affective states; it should also include a state of good physical health and ensuring that many if not all needs of the animal are being met in terms of natural drives’. The tension between the concepts of hedonic positive welfare and wellbeing can be reduced to the following question: ‘Is hedonia the common currency for evaluating all physical and mental performance in the animal’s life?’ The provisional answer from research on wellbeing is as follows: ‘No. Eudaimonic and social functions confer benefits that can be cashed out by the animal in currencies other than hedonia.’. This viewpoint is illustrated in the discussion by Beck and Gregorini (2020) of the distinct eudaimonic and hedonic benefits of dietary complexity in ruminants. Rault *et al.* (2020, p. 5) recognised the potential value of the concept of eudaimonia to the study of positive welfare by noting the following: ‘Although eudaimonia does not appear to have found its way into the animal welfare science literature yet, it could become a third view. A hindrance may be the feasibility of its operationalisation, given that the study of hedonic pleasure is more accessible with the current tools available (e.g. in behavioural biology) than the study of eudaimonic happiness, especially as approaches to eudaimonia in humans to date rely on self-report.'. The conventional view that the subjective experience by the animal of its emotional state is the indivisible unit and common currency of its welfare has very strong foundations in behaviour, neuroscience and physiology (Cabanac 1992; Bracke *et al.* 1999*b*; Boissy *et al.* 2007; Budaev *et al.* 2020). It is hoped that new information on variability in functional integrity and its relationships with other positive outcomes can help clarify these concepts.

Previous authors have recognised integrity as an aspect of welfare (e.g. Verhoog 2000). It is hoped that new measures of the stability of system functions can extend previous methods for assessment of change in system functions (Barnett and Hemsworth 1990) to help operationalise integrity as an indicator of positive welfare and wellbeing.

It is suggested that the conventional compartment approach grounded in reductionist diagnostic methodologies for identifying causes and remedies for harms and deficiencies can be complemented by structural analyses as a strategy for determining the integrity of functional outcomes. The wide diversity of other methodologies for measuring indicators of welfare already in use is not excluded by this approach. A continuum exists between inputs and outcomes in the influence of negatives and positives such that lower-level outcomes linked to comfort, pleasure, confidence, interest, and a healthy life are important to quantify, as well as the higher-level outcomes indicative of systemic functional integrity.

Applying the framework

Frameworks provide a generic outline of the conceptual constructs they address and can require adaptation to the species, life stage, production system and environment in which animals are managed during their operationalisation through assessment protocols (Stygar *et al.* 2022). Detailed examples of this process of adaptation and validation are demonstrated by the EU WelfareQuality® protocol for dairy cattle (Knierim *et al.* 2021), the New Zealand beef cow–calf welfare assessment protocol (Kaurivi *et al.* 2019, 2020*a*, 2020*b*) and the Salmon Welfare Index Model (Stien *et al.* 2013; Pettersen *et al.* 2014). While frameworks do not dictate the specific variables that need to be assessed nor the interpretation of the statistics generated by analysis of measurements, analyses, nonetheless, contribute to validation and refinement of the constructs incorporated within a framework (Appleby and Sandøe 2002; Waiblinger *et al.* 2006). This process of validation and refinement is illustrated in detail for the development of an survey instrument for assessing emotional predisposition in dogs (Sheppard and Mills 2002). Similarly, it is likely that analyses of sensor data will help refine the concepts of positive welfare and wellbeing and are likely to lead to a more detailed differentiation of aspects of these constructs than has been achieved in animals to date. It is hoped the framework can help orientate these new descriptions of biological integrity in farm animals within the broader literature on welfare and wellbeing. To aid this process, a synopsis of some similarities and differences between welfare and wellbeing is presented in Fig. 7. The complex challenge of combining and reporting indicators also needs consideration (Sandøe *et al.* 2019).

Some limitations of the concepts and framework

The narrative description that eudaimonic wellbeing entails the attainment of inherited and developmentally acquired potential aligns with the concept that wellbeing is attained through perfectionism described by Appleby and Sandøe (2002) as fulfilment of an objective list of functional capabilities. Animals inherit and can developmentally acquire the potential to attain a diversity of skills and performance attributes. However, not all of these attributes may be achievable by a single member of a species despite the animal's potential to attain any particular favourable attribute if provided with an appropriate environment. This draws into question what constitutes fulfilment of the individual's potential to express positive health and a thriving mental and physical constitution. Is 'fulfilment' and 'attainment of potential' achieved through maximising all potential performance attributes? The proposition that wellbeing is realised as integrity of physical and psychological functions helps shift the concept of wellbeing from maximisation of all favourable attributes to dynamic stability of those that are attained. The range of the animal's inherited and developmentally acquired potentials for performance and the degree to which each of these potentials is fulfilled has implications for the concept of telos (Beck and Gregorini 2020), which is not further explored here.

The studies of day-to-day variability in production animals described above have found that animals differ in their ability to maintain integrity of biological functions and that a portion of that variation is heritable. This observation is consistent with a large body of work on persistent physiological and behavioural differences among individuals (for reviews, see Careau *et al.* 2008; Richter and Hintze 2019). Two implications here are (1) the potential to breed resilient animals that are better suited to coping with the production environment, and (2) the recognition that any fine-grained metric of resilience, integrity or wellbeing is likely to detect residual differences among individuals, whatever the environment animals have access to. A more fundamental question here is whether a capacity to maintain integrity of function in all environments and during all life-stage

Heritage	Biology	Philosophy
Precepts	'Drives' arising from needs and wants generate behaviours and mental states in support of biological functions Deprivations, and physical and psychological insults cause suffering Positive environmental engagement can invoke positive affective states	Animals have the potential to develop competences that enable physical and mental fulfilment through harmonious environmental engagement
Construct	**Welfare**	**Wellbeing**
What is it?	The physical and mental experiences arising from engaging with the environment	Fulfillment of potential for environmental mastery, purpose, pleasure, and connectedness achieved through engaging with the environment
Model	Physical functions, mental state, natural living	Eudaimonia, hedonia, social wellbeing
Frameworks	Five Freedoms, Five Domains, Good Life, OIE Welfare Principles	Doing, feeling, interacting (connecting)
Assessment schemes	e.g. WelfareQuality®, AssureWel, RSPCA Assured, SWIM	None are explicitly aligned yet with the three-factor model of wellbeing. The Good Life and Five Domains frameworks implicitly adopt many of these concepts without articulating them within the three-factor model
What is measured?	Availability of resources to enable fulfilment of freedoms. Physical and mental outcomes to determine whether individual freedoms and positively-valenced mental states are realised	Provisionally, the integrity of physical, behavioural and mental activities (trajectories, rhythmicity, complexity) to determine whether harmonious environmental engagement is being achieved
Temporal focus	Events (e.g. marking) and moments in time (e.g. snapshot surveys)	Long-term to whole-of-life
Commonalities	Role of positive experiences in generating a positively-valenced hedonic affective state	
'Currencies' for evaluating positives	Affective experience	Functional integrity, affective experience, social connectedness
Biological outcomes	Health and having what the animal wants	Fulfilment of the individual's potential to express positive health and a thriving mental and physical constitution

Fig. 7. An outline of the concepts of Welfare and Wellbeing.

transitions is a desirable characteristic for the animal to express. Relationships among robustness, phenotypic plasticity and global indicators of functional integrity require further consideration.

The discussion has focused on welfare and wellbeing of the individual; yet it is well recognised that attributes assessed at the level of the group are influenced by the current characteristics of individuals such as their disease status (Doeschl-Wilson *et al.* 2021) as well as by heritable characteristics of the individual through indirect genetic effects (Bergsma *et al.* 2008; Camerlink *et al.* 2018). Individuals can both enhance and diminish the wellbeing of others in a group, and optimising the wellbeing of the individual and the group may not be mutually attainable goals (Fraser 2003; Hemsworth *et al.* 2015), Thus, there is a need for concepts and their explanatory frameworks to include descriptions of welfare and wellbeing at both the group and individual level. This is not attempted with the current framework. If appropriate metrics of social connectedness can be developed, they may capture some of the wellbeing attributes of the group. Health dynamics can also differ between the group and the individual and need inclusion within a more comprehensive framework (Knap and Doeschl-Wilson 2020; Doeschl-Wilson *et al.* 2021).

Conclusions

Philosophical deliberations and empirical evidence suggest that positive welfare and wellbeing is not a one-dimensional state that can be assessed via a single indicator. Continuous changes in the environment require dynamic engagement by the animal to minimise disturbances to its vital functions. Some environmental fluctuations can be accommodated through prediction and control, whereas others need to be managed through deploying resources to defence and repair. Measures of the dynamic day-to-day integrity of biological functions can provide indicators of the success of the animal in attaining mastery of its environment and sustaining a thriving mental and physical constitution. New information on functional integrity enabled by sensor technologies has the capacity to extend our understanding of positive biology and the dynamic status of the individual's welfare and wellbeing. A framework is proposed for integrating this information into existing models for describing and assessing welfare and wellbeing.

References

Adriaens I, Friggens NC, Ouweltjes W, Scott H, Aernouts B, Statham J (2020) Productive life span and resilience rank can be predicted from on-farm first-parity sensor time series but not using a common equation across farms. *Journal of Dairy Science* **103**, 7155–7171. doi:10.3168/jds.2019-17826

Appleby MC, Sandøe P (2002) Philosophical debate on the nature of well-being: implications for animal welfare. *Animal Welfare* **11**, 283–294.

Asher L, Collins LM, Ortiz-Pelaez A, Drewe JA, Nicol CJ, Pfeiffer DU (2009) Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *Journal of the Royal Society Interface* **6**, 1103–1119. doi:10.1098/rsif.2009.0221

Ayres JS (2020) The biology of physiological health. *Cell* **181**, 250–269. doi:10.1016/j.cell.2020.03.036

Barnett JL, Hemsworth PH (1990) The validity of physiological and behavioural measures of animal welfare. *Applied Animal Behaviour Science* **25**, 177–187. doi:10.1016/0168-1591(90)90079-S

Beck MR, Gregorini P (2020) How dietary diversity enhances hedonic and eudaimonic well-being in grazing ruminants. *Frontiers in Veterinary Science* **7**, 191. doi:10.3389/fvets.2020.00191

Bedere N, Berghof TVL, Peeters K, Pinard-van der Laan M-H, Visscher J, David I, Mulder HA (2022) Using egg production longitudinal recording to study the genetic background of resilience in purebred and crossbred laying hens. *Genetics Selection Evolution* **54**, 26. doi:10.1186/s12711-022-00716-8

Ben Abdelkrim A, Puillet L, Gomes P, Martin O (2021) Lactation curve model with explicit representation of perturbations as a phenotyping tool for dairy livestock precision farming. *Animal* **15**, 100074. doi:10.1016/j.animal.2020.100074

Berghof TVL, Poppe M, Mulder HA (2019*a*) Opportunities to improve resilience in animal breeding programs. *Frontiers in Genetics* **9**, 692. doi:10.3389/fgene.2018.00692

Berghof TVL, Bovenhuis H, Mulder HA (2019*b*) Body weight deviations as indicator for resilience in layer chickens. *Frontiers in Genetics* **10**, 1216. doi:10.3389/fgene.2019.01216

Bergsma R, Kanis E, Knol EF, Bijma P (2008) The contribution of social effects to heritable variation in finishing traits of domestic pigs (*Sus scrofa*). *Genetics* **178**, 1559–1570. doi:10.1534/genetics.107.084236

Boissy A, Manteuffel G, Jensen MB, Moe RO, Spruijt B, Keeling LJ, Winckler C, Forkman B, Dimitrov I, Langbein J, Bakken M, Veissier I, Aubert A (2007) Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior* **92**, 375–397. doi:10.1016/j.physbeh.2007.02.003

Botreau R, Veissier I, Butterworth A, Bracke MBM, Keeling LJ (2007) Definition of criteria for overall assessment of animal welfare. *Aimal Welfare* **16**, 225–228.

Bracke MBM, Spruijt BM, Metz JHM (1999*a*) Overall animal welfare assessment reviewed. Part 1: is it possible? *Netherlands Journal of Agricultural Science* **47**, 279–291. doi:10.18174/njas.v47i3.466

Bracke MBM, Spruijt BM, Metz JHM (1999*b*) Overall animal welfare reviewed. Part 3: welfare assessment based on needs and supported by expert opinion. *Netherlands Journal of Agricultural Science* **47**, 307–322. doi:10.18174/njas.v47i3.468

Bracke MBM, Metz JHM, Spruijt BM (1999*c*) Overall animal welfare reviewed. Part 2: assessment tables and schemes. *Netherlands Journal of Agricultural Science* **47**, 293–305. doi:10.18174/njas.v47i3.467

Brambell FWR (1965) Report of the technical committee to enquire into the welfare of animals kept under intensive livestock husbandry systems. The Brambell Report. (Her Majesty's Stationary Office: London, UK)

Broom DM (1986) Indicators of poor welfare. *British Veterinary Journal* **142**, 524–526. doi:10.1016/0007-1935(86)90109-0

Budaev S, Kristiansen TS, Giske J, Eliassen S (2020) Computational animal welfare: towards cognitive architecture models of animal sentience, emotion and wellbeing. *Royal Society Open Science* **7**, 201886. doi:10.1098/rsos.201886

Buller H, Blokhuis H, Lokhorst K, Silberberg M, Veissier I (2020) Animal welfare management in a digital world. *Animals* **10**, 1779. doi:10.3390/ani10101779

Cabanac M (1992) Pleasure: the common currency. *Journal of Theoretical Biology* **155**, 173–200. doi:10.1016/S0022-5193(05)80594-6

Camerlink I, Ursinus WW, Bartels AC, Bijma P, Bolhuis JE (2018) Indirect genetic effects for growth in pigs affect behaviour and weight around weaning. *Behavior Genetics* **48**, 413–420. doi:10.1007/s10519-018-9911-5

Capitanio JP, Mason WA (2019) Personality as adaptation: perspectives from nonhuman primates. In 'Using basic personality research to inform personality pathology'. (Eds DB Samuel, DR Lynam) pp. 219–236. (Oxford University Press: New York, NY, USA)

Careau V, Thomas D, Humphries MM, Réale D (2008) Energy metabolism and animal personality. *Oikos* **117**, 641–653. doi:10.1111/j.0030-1299.2008.16513.x

Casey TM, Plaut K, Boerman J (2022) Circadian clocks and their role in lactation competence. *Domestic Animal Endocrinology* **78**, 106680. doi:10.1016/j.domaniend.2021.106680

Coe JC (2017) Embedding environmental enrichment into zoo animal facility design. In 'Zoo design conference Wroclaw', 5–7 April 2017. (Eds A Mękarska, L Przybylska) pp. 1–21. Available at https://www.researchgate.net/publication/317357052 [Accessed 3 July 2022]

Colditz IG (2018) Objecthood, agency and mutualism in valenced farm animal environments. *Animals* **8**, 50. doi:10.3390/ani8040050

Colditz IG (2020) A consideration of physiological regulation from the perspective of Bayesian enactivism. *Physiology & Behavior* **214**, 112 758. doi:10.1016/j.physbeh.2019.112758

Colditz IG (2021) Adrenergic tone as an intermediary in the temperament syndrome associated with flight speed in beef cattle. *Frontiers in Animal Science* **2**, 652306. doi:10.3389/fanim.2021.652306

Colditz IG (2022) Competence to thrive: resilience as an indicator of positive health and positive welfare in animals. *Animal Production Science* **62**, 1439–1458. doi:10.1071/AN22061

Colditz IG, Hine BC (2016) Resilience in farm animals: biology, management, breeding and implications for animal welfare. *Animal Production Science* **56**, 1961–1983. doi:10.1071/AN15297

Dawkins MS (2006) Through animal eyes: what behaviour tells us. *Applied Animal Behaviour Science* **100**, 4–10. doi:10.1016/j.applanim.2006.04.010

Dawkins MS (2008) The science of animal suffering. *Ethology* **114**, 937–945. doi:10.1111/j.1439-0310.2008.01557.x

Dawkins MS (2021*a*) 'The science of animal welfare: understanding what animals want.' (Oxford University Press: USA)

Dawkins MS (2021*b*) Does smart farming improve or damage animal welfare? Technology and what animals want. *Frontiers in Animal Science* **2**, 736536. doi:10.3389/fanim.2021.736536

Deci EL, Ryan RM (2008) Hedonia, eudaimonia, and well-being: an introduction. *Journal of Happiness Studies* **9**, 1–11. doi:10.1007/s10902-006-9018-1

Doeschl-Wilson A, Knap PW, Opriessnig T, More SJ (2021) Review: livestock disease resilience: from individual to herd level. *Animal* **15**, 100286. doi:10.1016/j.animal.2021.100286

Duncan IJH, Dawkins MS (1983) The problem of assessing 'well-being' and 'suffering' in farm animals. In 'Indicators relevant to farm animal welfare. Vol. 23'. (Ed. D Smidt) pp. 13–24. (Springer: Dortrecht, Netherlands)

Düpjan S, Dawkins MS (2022) Animal welfare and resistance to disease: interaction of affective states and the immune system. *Frontiers in Veterinary Science* **9**, 929805. doi:10.3389/fvets.2022.929805

Edgar JL, Mullan SM, Pritchard JC, McFarlane UJC, Main DCJ (2013) Towards a 'good life' for farm animals: development of a resource tier framework to achieve positive welfare for laying hens. *Animals* **3**, 584–605. doi:10.3390/ani3030584

Elgersma GG, de Jong G, van der Linde R, Mulder HA (2018) Fluctuations in milk yield are heritable and can be used as a resilience indicator to breed healthy cows. *Journal of Dairy Science* **101**, 1240–1250. doi:10.3168/jds.2017-13270

Farrelly C (2012) 'Positive biology' as a new paradigm for the medical sciences. *EMBO Reports* **13**, 186–188. doi:10.1038/embor.2011.256

FAWC (2009*a*) Five freedoms. Available at https://webarchive.nationalarchives.gov.uk/ukgwa/20121010012427/http://www.fawc.org.uk/freedoms.htm [Accessed 21 May 2022]

FAWC (2009*b*) Farm animal welfare in Great Britain: past, present and future. (Farm Animal Welfare Council). Available at https://www.gov.uk/government/publications/fawc-report-on-farm-animal-welfare-in-great-britain-past-present-and-future [Accessed 20 May 2022]

Fisher AJ, Medaglia JD, Jeronimus BF (2018) Lack of group-to-individual generalizability is a threat to human subjects research. *Proceedings of the National Academy of Sciences* **115**, E6106–E6115. doi:10.1073/pnas.1711978115

Fraser D (1999) Animal ethics and animal welfare science: bridging the two cultures. *Applied Animal Behaviour Science* **65**, 171–189. doi:10.1016/S0168-1591(99)00090-8

Fraser D (2003) Assessing animal welfare at the farm and group level: the interplay of science and values. *Animal Welfare* **12**, 433–443.

Fraser D (2008) Understanding animal welfare. *Acta Veterinaria Scandinavica* **50**, S1. doi:10.1186/1751-0147-50-S1-S1

Fraser D, Duncan IJH, Edwards SA, Grandin T, Gregory NG, Guyonnet V, Hemsworth PH, Huertas SM, Huzzey JM, Mellor DJ, Mench JA, Špinka M, Whay HR (2013) General principles for the welfare of animals in production systems: the underlying science and its application. *The Veterinary Journal* **198**, 19–27. doi:10.1016/j.tvjl.2013.06.028

Freund J, Brandmaier AM, Lewejohann L, Kirste I, Kritzler M, Krüger A, Sachser N, Lindenberger U, Kempermann G (2013) Emergence of individuality in genetically identical mice. *Science* **340**, 756–759. doi:10.1126/science.1235294

Friggens NC, Blanc F, Berry DP, Puillet L (2017) Review: Deciphering animal robustness. A synthesis to facilitate its use in livestock breeding and management. *Animal* **11**, 2237–2251. doi:10.1017/S175173111700088X

Friggens NC, Adriaens I, Boré R, Cozzi G, Jurquet J, Kamphuis C, Leiber F, Lora I, Sakowski T, Statham J, De Haas Y (2022) Resilience: reference measures based on longer-term consequences are needed to unlock the potential of precision livestock farming technologies for quantifying this trait. *Peer Community Journal* **2**, e38. doi:10.24072/pcjournal.136.

Garcia-Baccino CA, Marie-Etancelin C, Tortereau F, Marcon D, Weisbecker J-L, Legarra A (2021) Detection of unrecorded environmental challenges in high-frequency recorded traits, and genetic determinism of resilience to challenge, with an application on feed intake in lambs. *Genetics Selection Evolution* **53**, 4. doi:10.1186/s12711-020-00595-x

Grandin T (2004) Principles for handling grazing animals. In 'The well-being of farm animals'. (Eds GJ Benson, BE Rollin) pp. 119–143. (Blackwell Publishing)

Haslbeck JMB, Ryan O (2022) Recovering within-person dynamics from psychological time series. *Multivariate Behavioral Research* **57**, 735–766. doi:10.1080/00273171.2021.1896353

Heino MTJ, Knittle K, Noone C, Hasselman F, Hankonen N (2021) Studying behaviour change mechanisms under complexity. *Behavioral Sciences* **11**, 77. doi:10.3390/bs11050077

Hemsworth PH, Mellor DJ, Cronin GM, Tilbrook AJ (2015) Scientific assessment of animal welfare. *New Zealand Veterinary Journal* **63**, 24–30. doi:10.1080/00480169.2014.966167

Hurnik JF (1988) Welfare of farm animals. *Applied Animal Behaviour Science* **20**, 105–117. doi:10.1016/0168-1591(88)90130-X

Iung LHdS, Carvalheiro R, Neves HHdR, Mulder HA (2020) Genetics and genomics of uniformity and resilience in livestock and aquaculture species: a review. *Journal of Animal Breeding and Genetics* **137**, 263–280. doi:10.1111/jbg.12454

Johnson AK, Rault J-L, Marchant JN, Baxter EM, O'Driscoll K (2022) Improving young pig welfare on-farm: the five domains model. *Journal of Animal Science* **100**, 1–15. doi:10.1093/jas/skac164

Kaurivi YB, Laven R, Hickson R, Stafford K, Parkinson T (2019) Identification of suitable animal welfare assessment measures for extensive beef systems in New Zealand. *Agriculture* **9**, 66. doi:10.3390/agriculture9030066

Kaurivi YB, Hickson R, Laven R, Parkinson T, Stafford K (2020*a*) Developing an animal welfare assessment protocol for cows in extensive beef cow-calf systems in New Zealand. Part 2: categorisation and scoring of welfare assessment measures. *Animals* **10**, 1592. doi:10.3390/ani10091592

Kaurivi YB, Laven R, Hickson R, Parkinson T, Stafford K (2020*b*) Developing an animal welfare assessment protocol for cows in extensive beef cow–calf systems in New Zealand. Part 1: assessing the feasibility of identified animal welfare assessment measures. *Animals* **10**, 1597. doi:10.3390/ani10091597

Keeling LJ, Winckler C, Hintze S, Forkman B (2021) Towards a positive welfare protocol for cattle: a critical review of indicators and suggestion of how we might proceed. *Frontiers in Animal Science* **2**, 753080. doi:10.3389/fanim.2021.753080

Knap PW (2005) Breeding robust pigs. *Australian Journal of Experimental Agriculture* **45**, 763–773. doi:10.1071/EA05041

Knap PW, Doeschl-Wilson A (2020) Why breed disease-resilient livestock, and how? *Genetics Selection Evolution* **52**, 60. doi:10.1186/s12711-020-00580-4

Knierim U, Winckler C, Mounier L, Veissier I (2021) Developing effective welfare measures for cattle. In 'Understanding the behaviour and improving the welfare of dairy cattle.' (Ed. M Endres) pp. 81–102. (Burleigh Dodds Science Publishing)

Koolhaas JM (2008) Coping style and immunity in animals: making sense of individual variation. *Brain, Behavior, and Immunity* **22**, 662–667. doi:10.1016/j.bbi.2007.11.006

Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews* **23**, 925–935. doi:10.1016/S0149-7634(99)00026-3

Korte SM, Olivier B, Koolhaas JM (2007) A new animal welfare concept based on allostasis. *Physiology & Behavior* **92**, 422–428. doi:10.1016/j.physbeh.2006.10.018

Kristiansen TS, Fernö A (2020) The predictive brain: perception turned upside down. In 'The welfare of fish'. (Eds TS Kristiansen, A Fern, MA Pavlidis, H van de Vis) pp. 211–227. (Springer: Cham, Switzerland)

Lawrence AB, Vigors B, Sandøe P (2019) What is so positive about positive animal welfare? Critical review of the literature. *Animals* **9**, 783. doi:10.3390/ani9100783

Lenoir G, Muñoz-Tamayo R, Flatres-Grall L, David I, Friggens NC (2022) Towards the characterisation of animal robustness by dynamic energy allocation indicators in fattening pigs. In 'World congress on genetics applied to livestock production. Rotterdam'. (Eds Y de Haas, RF veerkamp) p. 09_010. (Wageningen Academic Publishers)

Lomas T (2016) Positive psychology – the second wave. *The Psychologist* **29**, 536–539.

Lyons DM, Schatzberg AF (2020) Resilience as a process instead of a trait. In 'Stress resilience'. (Ed. A Chen) pp. 33–44. (Academic Press: London, UK)

Mackay TFC, Stone EA, Ayroles JF (2009) The genetics of quantitative traits: challenges and prospects. *Nature Reviews Genetics* **10**, 565–577. doi:10.1038/nrg2612

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 animal welfare thinking: moving beyond the 'Five Freedoms' towards "a Life Worth Living". *Animals* **6**, 21. doi:10.3390/ani6030021

Mellor DJ (2017) Operational details of the five domains model and its key applications to the assessment and management of animal welfare. *Animals* **7**, 60. doi:10.3390/ani7080060

Mellor DJ, Beausoleil NJ (2015) Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare* **24**, 241–253. doi:10.7120/09627286.24.3.241

Mellor DJ, Reid CSW (1994) Concepts of animal well-being and predicting the impact of procedures on experimental animals. In 'Improving the well-being of animals in the research environment'. (Eds RM Baker, G Jenkin, DJ Mellor) pp. 3–18. (Australian and New Zealand Council for the Care of Animals in Research and Teaching)

Mendl M, Burman OHP, Paul ES (2010) An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences* **277**, 2895–2904. doi:10.1098/rspb.2010.0303

Mengistu UL, Puchala R, Sahlu T, Gipson TA, Dawson LJ, Goetsch AL (2017) Conditions to evaluate differences among individual sheep and goats in resilience to high heat load index. *Small Ruminant Research* **147**, 89–95. doi:10.1016/j.smallrumres.2016.12.039

Mengistu SB, Mulder HA, Bastiaansen JWM, Benzie JAH, Khaw HL, Trinh TQ, Komen H (2022) Fluctuations in growth are heritable and a potential indicator of resilience in Nile tilapia (*Oreochromis niloticus*). *Aquaculture* **560**, 738481. doi:10.1016/j.aquaculture.2022.738481

Miller LJ, Vicino GA, Sheftel J, Lauderdale LK (2020) Behavioral diversity as a potential indicator of positive animal welfare. *Animals* **10**, 1211. doi:10.3390/ani10071211

Mormède P, Foury A, Terenina E, Knap PW (2011) Breeding for robustness: the role of cortisol. *Animal* **5**, 651–657. doi:10.1017/S1751731110002168

Nordenfelt L (2006) 'Animal and human health and welfare: a comparative philosophical analysis.' (CABI: Wallingford, UK)

Nordenfelt L (2011) Health and welfare in animals and humans. *Acta Biotheoretica* **59**, 139–152. doi:10.1007/s10441-011-9125-1

Nunes Marsiglio Sarout B, Waterhouse A, Duthie C-A, Candal Poli CHE, Haskell MJ, Berger A, Umstatter C (2018) Assessment of circadian rhythm of activity combined with random regression model as a novel approach to monitoring sheep in an extensive system. *Applied Animal Behaviour Science* **207**, 26–38. doi:10.1016/j.applanim.2018.06.007

OIE (2021) Terrestrial code for animal health. Available at https://www.oie.int/en/what-we-do/standards/codes-and-manuals/terrestrial-code-online-access/ [Accessed 17 May 2022]

Parois SP, Van Der Zande LE, Knol EF, Kemp B, Rodenburg TB, Bolhuis JE (2022*a*) A multi-suckling system combined with an enriched housing environment during the growing period promotes resilience to various challenges in pigs. *Scientific Reports* **12**, 6804. doi:10.1038/s41598-022-10745-4

Parois SP, Van Der Zande LE, Knol EF, Kemp B, Rodenburg TB, Bolhuis JE (2022*b*) Effects of a multi-suckling system combined with enriched housing post-weaning on response and cognitive resilience to isolation. *Frontiers in Veterinary Science* **9**, 868149. doi:10.3389/fvets.2022.868149

Pettersen JM, Bracke MBM, Midtlyng PJ, Folkedal O, Stien LH, Steffenak H, Kristiansen TS (2014) Salmon welfare index model 2.0: an extended model for overall welfare assessment of caged Atlantic salmon, based on a review of selected welfare indicators and intended for fish health professionals. *Reviews in Aquaculture* **6**, 162–179. doi:10.1111/raq.12039

Pomerantz O, Capitanio JP (2021) Temperament predicts the quality of social interactions in captive female rhesus macaques (*Macaca mulatta*). *Animals* **11**, 2452. doi:10.3390/ani11082452

Poppe M, Veerkamp RF, van Pelt ML, Mulder HA (2020) Exploration of variance, autocorrelation, and skewness of deviations from lactation curves as resilience indicators for breeding. *Journal of Dairy Science* **103**, 1667–1684. doi:10.3168/jds.2019-17290

Poppe M, Mulder HA, Kamphuis C, Veerkamp RF (2021*a*) Between-herd variation in resilience and relations to herd performance. *Journal of Dairy Science* **104**, 616–627. doi:10.3168/jds.2020-18525

Poppe M, Mulder HA, Veerkamp RF (2021*b*) Validation of resilience indicators by estimating genetic correlations among daughter groups and with yield responses to a heat wave and disturbances at herd level. *Journal of Dairy Science* **104**, 8094–8106. doi:10.3168/jds.2020-19817

Putz AM, Harding JCS, Dyck MK, Fortin F, Plastow GS, Dekkers JCM, PigGen Canada (2019) Novel resilience phenotypes using feed intake data from a natural disease challenge model in wean-to-finish pigs. *Frontiers in Genetics* **9**, 660. doi:10.3389/fgene.2018.00660

Rault J-L, Hintze S, Camerlink I, Yee JR (2020) Positive welfare and the like: distinct views and a proposed framework. *Frontiers in Veterinary Science* **7**, 370. doi:10.3389/fvets.2020.00370

Reid J, Nolan A, Scott M (2022) Application of psychometrics to assess quality of life in animals. In 'Bridging research disciplines to advance animal welfare science: a practical guide.' (Ed. I Camerlink) pp. 125–140. (CAB International: Wallingford, UK)

Revilla M, Friggens NC, Broudiscou LP, Lemonnier G, Blanc F, Ravon L, Mercat MJ, Billon Y, Rogel-Gaillard C, Le Floch N, Estellé J, Muñoz-Tamayo R (2019) Towards the quantitative characterisation of piglets' robustness to weaning: a modelling approach. *Animal* **13**, 2536–2546. doi:10.1017/S1751731119000843

Richter SH, Hintze S (2019) From the individual to the population – and back again? Emphasising the role of the individual in animal welfare science. *Applied Animal Behaviour Science* **212**, 1–8. doi:10.1016/j.applanim.2018.12.012

Rowe E, Mullan S (2022) Advancing a 'Good Life' for farm animals: development of resource tier frameworks for on-farm assessment of positive welfare for beef cattle, broiler chicken and pigs. *Animals* **12**, 565. doi:10.3390/ani12050565

Rowland T, Pike TW, Burman OHP (2021) A network perspective on animal welfare. *Animal Welfare* **30**, 235–248. doi:10.7120/09627286.30.3.001

Ryff CD (2022) Positive psychology: looking back and looking forward. *Frontiers in Psychology* **13**, 840062. doi:10.3389/fpsyg.2022.840062

Ryff CD, Singer BH, Dienberg Love G (2004) Positive health: connecting well-being with biology. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**, 1383–1394. doi:10.1098/rstb.2004.1521

Ryff CD, Boylan JM, Kirsch JA (2021) Eudaimonic and hedonic well-being: an integrative perspective with linkages to sociodemographic factors and health. In 'Measuring well-being.' (Eds MT Lee, LD Kubzansky, TJ VanderWeele) pp. 92–135. (Oxford University Press)

Sandøe P, Corr SA, Lund TB, Forkman B (2019) Aggregating animal welfare indicators: can it be done in a transparent and ethically robust way? *Animal Welfare* **28**, 67–76. doi:10.7120/09627286.28.1.067

Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. *Nature* **461**, 53–59. doi:10.1038/nature08227

Scheffer M, Bolhuis JE, Borsboom D, Buchman TG, Gijzel SMW, Goulson D, Kammenga JE, Kemp B, van de Leemput IA, Levin S, Martin CM, Melis RJF, van Nes EH, Romero LM, Olde Rikkert MGM (2018) Quantifying resilience of humans and other animals. *Proceedings of the National Academy of Sciences* 115, 11883–11890. 10.1073/pnas.1810630115

Scheibe KM, Berger A, Langbein J, Streich WJ, Eichhorn K (1999) Comparative analysis of ultradian and circadian behavioural rhythms for diagnosis of biorhythmic state of animals. *Biological Rhythm Research* **30**, 216–233. doi:10.1076/brhm.30.2.216.1420

Sheppard G, Mills DS (2002) The development of a psychometric scale for the evaluation of the emotional predispositions of pet dogs.

International Journal of Comparative Psychology **15**, 201–222. doi:10.46867/C4G30W
Stafleu FR, Grommers FJ, Vorstenbosch J (1996) Animal welfare: evolution and erosion of a moral concept. *Animal Welfare* **5**, 225–234.
Sterling P (2012) Allostasis: a model of predictive regulation. *Physiology & Behavior* **106**, 5–15. doi:10.1016/j.physbeh.2011.06.004
Stien LH, Bracke MBM, Folkedal O, Nilsson J, Oppedal F, Torgersen T, Kittilsen S, Midtlyng PJ, Vindas MA, Øverli Ø, Kristiansen TS (2013) Salmon Welfare Index Model (SWIM 1.0): a semantic model for overall welfare assessment of caged Atlantic salmon: review of the selected welfare indicators and model presentation. *Reviews in Aquaculture* **5**, 33–57. doi:10.1111/j.1753-5131.2012.01083.x
Stygar AH, Krampe C, Llonch P, Niemi JK (2022) how far are we from data-driven and animal-based welfare assessment? A critical analysis of European quality schemes. *Frontiers in Animal Science* **3**, 874260. doi:10.3389/fanim.2022.874260
Sun D, Webb L, van der Tol PPJ, van Reenen K (2021) A systematic review of automatic health monitoring in calves: glimpsing the future from current practice. *Frontiers in Veterinary Science* **8**, 761468. doi:10.3389/fvets.2021.761468
Torgerson-White L, Sánchez-Suárez W (2022) Looking beyond the Shoal: fish welfare as an individual attribute. *Animals* **12**, 2592. doi:10.3390/ani12192592
Turner PV (2019) Moving beyond the absence of pain and distress: focusing on positive animal welfare. *ILAR Journal* **60**, 366–372. doi:10.1093/ilar/ilaa017
van Dixhoorn IDE, de Mol RM, van der Werf JTN, van Mourik S, van Reenen CG (2018) Indicators of resilience during the transition period in dairy cows: a case study. *Journal of Dairy Science* **101**, 10271–10282. doi:10.3168/jds.2018-14779
Veissier I, Jensen KK, Botreau R, Sandøe P (2011) Highlighting ethical decisions underlying the scoring of animal welfare in the Welfare Quality® scheme. *Animal Welfare* **20**, 89–101.
Verhoog H (2000) Defining positive welfare and animal integrity. In 'Diversity of livestock systems and definition of animal welfare'. (Eds M Hovi, MG Trujillo) pp. 108–119. (University of Reading Reading)
Vigors B, Sandøe P, Lawrence AB (2021) Positive welfare in science and society: differences, similarities and synergies. *Frontiers in Animal Science* **2**, 738193. doi:10.3389/fanim.2021.738193
Wagner N, Mialon M-M, Sloth KH, Lardy R, Ledoux D, Silberberg M, de Boyer des Roches A, Veissier I (2021) Detection of changes in the circadian rhythm of cattle in relation to disease, stress, and reproductive events. *Methods* **186**, 14–21. doi:10.1016/j.ymeth.2020.09.003
Waiblinger S, Boivin X, Pedersen V, Tosi M-V, Janczak AM, Visser EK, Jones RB (2006) Assessing the human–animal relationship in farmed species: a critical review. *Applied Animal Behaviour Science* **101**, 185–242. doi:10.1016/j.applanim.2006.02.001
Wampfler R, Klingler S, Solenthaler B, Schinazi VR, Gross M, Holz C (2022) Affective state prediction from smartphone touch and sensor data in the wild. In 'CHI'22: proceedings of the 2022 CHI conference on human factors in computing systems'. (Association for Computing Machinery)
Webber S, Cobb ML, Coe J (2022) Welfare through competence: a framework for animal-centric technology design. *Frontiers in Veterinary Science* **9**, 885973. doi:10.3389/fvets.2022.885973
Webster J (2013) International standards for farm animal welfare: science and values. *The Veterinary Journal* **198**, 3–4. doi:10.1016/j.tvjl.2013.08.034
Webster J (2016) Animal welfare: freedoms, dominions and 'A Life Worth Living'. *Animals* **6**, 35. doi:10.3390/ani6060035
Webster J (2021) Green milk from contented cows: is it possible? *Frontiers in Animal Science* **2**, 667196. doi:10.3389/fanim.2021.667196
Weinans E, Quax R, van Nes EH, van de Leemput IA (2021) Evaluating the performance of multivariate indicators of resilience loss. *Scientific Reports* **11**, 9148. doi:10.1038/s41598-021-87839-y
Wemelsfelder F, Hunter TEA, Mendl MT, Lawrence AB (2001) Assessing the 'whole animal': a free choice profiling approach. *Animal Behaviour* **62**, 209–220. doi:10.1006/anbe.2001.1741
WHO (1946) Constitution of the World Health Organization. Available at https://www.who.int/about/governance/constitution [Accessed 9 June 2022]
Williams LA (2021) From human wellbeing to animal welfare. *Neuroscience & Biobehavioral Reviews* **131**, 941–952. doi:10.1016/j.neubiorev.2021.09.014
Yeates JW (2011) Is 'a life worth living' a concept worth having? *Animal Welfare* **20**, 397–406.
Yeates JW, Main DCJ (2008) Assessment of positive welfare: a review. *The Veterinary Journal* **175**, 293–300. doi:10.1016/j.tvjl.2007.05.009

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