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Competence to thrive: resilience as an indicator of positive health and positive welfare in animals

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ABSTRACT

A capacity for an animal to maintain or regain healthy functioning in the face of environmental disturbances is recognised as resilience. For the individual animal, dynamic properties of the trajectory of performance traits (e.g. daily milk yield), periodicity of physiological and behavioural variables (e.g. body temperature) and complexity of biological functions (e.g. behavioural repertoire) can provide indicators of its resilience. These indicators provide a view of the individual's attempts to cope physically (and emotionally) with its non-shared micro-environment. The concept of resilience is examined as a multifaceted attribute that is hidden from direct measurement. The challenges for establishing relationships between general resilience and context-specific resilience such as disease resilience are explored by comparison with the multifaceted construct of temperament (personality). Lower variance in deviations from performance trajectories and stronger periodicity in rhythmic physiological and behavioural variables are mostly heritable and favourably associated with health and longevity. In humans, wellbeing is associated with health outcomes, and biomarkers of health are more strongly associated with eudaimonic than hedonic wellbeing. The psychological state of eudaimonia is associated with the capacity to express agency, function well, fulfill biological potential and express environmental mastery. The need for indicators of eudaimonia in animals has been suggested previously. Links between environmental mastery and the capacity to develop and express physiological, immune, behavioural, cognitive and affective competencies are examined. It is suggested that longitudinal data on individual animals can provide a precision physical indicator of eudaimonic positive welfare. In this view, positive welfare entails both eudaimonic and hedonic aspects of wellbeing, neither of which is alone sufficient to describe or to maximise positive welfare. Cumulative scores of resilience may have utility for assessing the lifetime welfare experience of the individual and when summed at the farm level may provide a metric for benchmarking welfare performance. Breeding for resilience selects for normativity of biological functions assessed against the individual animal's own baseline of inherited and developmentally acquired potential. This differs from current approaches to selection for production, which aim to maximise production or production efficiency benchmarked against the group mean. Biological costs and trade-offs for resilience require further research.

Keywords: affect, allostasis, arousal, behavioural complexity, biorhythms, construct validation, eudaimonia, hedonia, homeorhesis, homeostasis, latent construct, personality, positive health, positive welfare, precision welfare assessment, quality of life, stress, temperament, valence.

Introduction

Since the emergence of animal welfare in the 1960s as an issue of strong public concern, welfare has been considered in broad terms to include the physical and mental wellbeing of the animal. The Brambell report into the welfare of intensively housed livestock (Brambell 1965, p. 9) suggested that 'Welfare is a wide term that embraces both the physical and mental well-being of the animal. Any attempt to evaluate welfare … 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.'. Many public

submissions to the Brambell committee considered that growth rate of meat animals and egg production by hens were 'the only reliable objective measures of their welfare' (Brambell 1965). Nonetheless, the committee concluded that 'Growth … can be a pathological symptom, although it is more often a mark of health. Growth rate and condition … together are a better guide … but are not inconsistent with periods of acute, but transitory, physical or mental sufferin. principal cause of suffering in animals … is disease' (p. 11). Reflecting this sentiment, Hurnik and Lehman (1988) noted that production traits such as milk yield that underpin the commercial value of a farm animal represent only one aspect of its biological functioning. Normality of production, reproduction, immune function and behaviour, together with the presence of physiological and behavioural indicators of pleasure were all considered necessary for an animal to possess good welfare (Broom 1996). Failure to express these activities was a sign that the animal was coping poorly with its environment and in a state of poor welfare (Broom 1996; Mellor 2016). Misgivings about production as a singular measure of welfare (e.g. Duncan and Dawkins 1983; Broom 1986) were reinforced by the observation of many undesirable side-effects on health, immune function, metabolic functions and reproduction that accompany genetic selection for production efficiency in pigs, chickens and dairy cows (Rauw *et al.* 1998). Selection for productivity, these authors suggested, reduces allocation of resources to fitness functions in the animal and diminishes its capacity to maintain a homeostatic balance and to cope with environmental challenges (Rauw *et al.* 1998). As described in more detail below, recent years have seen a resurgence in the use of production variables to assess the capacity of animals to cope with environmental perturbations. This trend has been enabled by large datasets containing high frequency records of behavioural, physiological and production variables of individual animals (e.g. Neethirajan *et al.* 2017; Brito *et al.* 2020; Sun *et al.* 2021). Assessments at the level of the individual animal of dynamic properties of the trajectory of performance traits such as milk yield, periodicity of physiological and behavioural variables, and complexity of biological functions such as behavioural repertoires are being interpreted as (1) evidence of resilience to environmental perturbations, (2) an indicator of welfare, and (3) an avenue for improving health and welfare through genetic selection (Scheibe *et al.* 1999; Colditz and Hine 2016; Nunes Marsiglio Sarout *et al.* 2018; van Dixhoorn *et al.* 2018; Berghof *et al.* 2019b; Iung *et al.* 2019; Wagner *et al.* 2021; Bai and Plastow 2022). One aim of this review was to examine the merits of these inferences.

The concept of animal welfare has been consolidated to a tripartite model that encompasses three broad perspectives, namely, biological function, natural living, and affective state (Fraser *et al.* 1997; Fraser 2008; Mellor 2016), although limitations of the model are recognised (Weary and Robbins 2019). Welfare has been described in the following terms: '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' (italics in original, Fraser 1999, p. 178). These perspectives are represented in the principles of the Five Freedoms (Webster 2016), in the Five Domains framework (Mellor 2017) and in the dictum 'health and what animals want' (Dawkins 2021), and are implemented for assessment of welfare through programs such as WelfareQuality® (Botreau *et al.* 2007). Animal-based measures play a prominent role in welfare assessments and new methods for measuring biological function, natural living and affective state are being developed to complement theoretical and evidenced-based advances in understanding what animals are, what they can be, and how they function (Mellor 2016; Buller *et al.* 2020; Duncan 2020). Advances in the concept of animal resilience and new methods for its measurement are a part of this dynamic (Hine *et al.* 2015; Colditz and Hine 2016; Friggens *et al.* 2017; van Dixhoorn *et al.* 2018; Berghof *et al.* 2019b; Brito *et al.* 2020; Ben Abdelkrim *et al.* 2021; Wagner *et al.* 2021; Bai and Plastow 2022).

Given past shortcomings of production as an indicator of welfare, what can newer measures of biological function reveal about the welfare state of production animals? This review examines the conceptual relationship among resilience, health and welfare, and the contribution that indicators of resilience based on production, physiology and behavioural data may be able to make to improving farm animal welfare. The review begins by examining recent research on resilience in production animals and methods for its assessment based on analysis of trajectories in production, physiological and behavioural performance. Persistence of performance trajectories, biorhythms and functional complexity, as opposed to change and adaptation in the face of environmental fluctuations, is described as a normative process grounded in homeorhetic physiological regulation. The relationships between beneficial health and welfare outcomes associated with indicators of resilience and the concepts of eudaimonic and hedonic wellbeing are then examined. It is suggested that inherited and developmentally aquired attributes of the animal that contribute to resilience not only minimise harms but also confer functional competence to thrive that can provide eudaimonic wellbeing, positive health and positive welfare outcomes to the animal. A framework is presented that links resilience and the eudaimonic dimension of wellbeing with the duration of affective experience. Eudaimonic wellbeing is described as the bridge that links animal welfare science with quantitiative studies on resilience phenotypes.

Resilience

Animals vary in their capacity to cope with variation in their environment (Broom 1996); however, variation in the environment is not intrinsically bad for animals. Indeed, all organisms strive to predict and control their environments and to synchronise their activities with variations in environmental conditions (Jensen and Toates 1997; Scheibe *et al.* 1999; Lyon 2015; Bruineberg *et al.* 2018; Colditz 2018; Kristiansen and Fernö 2020). In this view, environmental variation does not necessarily constitute an environmental challenge, perturbation or disturbance; rather it is environmental variation that cannot be predicted or controlled that poses a challenge to the animal (Jensen and Toates 1997; Lee *et al.* 2018; Kristiansen and Fernö 2020). A capacity for animals to be minimally affected by environmental disturbances or to rapidly recover from them is recognised as resilience (Hine *et al.* 2015; Tedeschi *et al.* 2015; Colditz and Hine 2016; Friggens *et al.* 2017; van Dixhoorn *et al.* 2018; Berghof *et al.* 2019b; Bai and Plastow 2022).

Resilience in livestock has been described in many contexts. A type of resilience appears to have been first recognised in farm animals as a distinction between resistance to infestation and resistance to the effects of infestation of sheep with the nematode parasite, *Haemonchus contortus* (Clunies Ross 1932). Resilience has been assessed in the context of nematode parasite infection (Albers *et al.* 1987; Bisset and Morris 1996; Kelly *et al.* 2013), microbial infection (Mulder and Rashidi 2017; Putz *et al.* 2019; van der Zande *et al.* 2020; Bai and Plastow 2022), high or low temperature exposure (Mengistu *et al.* 2017; Sánchez-Molano *et al.* 2020; Tsartsianidou *et al.* 2021), diet (Steel 2003), feed shortage (María *et al.* 2004), weaning (Hine *et al.* 2019; Revilla *et al.* 2019), routine management within the production environment (Meyer and Colditz 2015; Elgersma *et al.* 2018; Nunes Marsiglio Sarout *et al.* 2018; Nguyen-Ba *et al.* 2020; Poppe *et al.* 2020, 2021b; Sun *et al.* 2021; Bai and Plastow 2022), and the transition period in the dairy cow (van Dixhoorn *et al.* 2018), among other contexts (e.g. Bushby *et al.* 2018; Brito *et al.* 2020).

Historically, infectious diseases have attracted the strongest attention in studies of resilience in livestock. Resilience to infection is usually described as the relative level of production at a given level of infection and can be identified by comparison among animals or within an animal over time (Bishop 2012; Knap and Doeschl-Wilson 2020; Bai and Plastow 2022). It is distinguished from resistance, which is described as the relative level of infection an animal develops at a given level of pathogen exposure. Tolerance to infection is described as the sensitivity of production to a change in the level of infection (Simms 2000; Bishop 2012; Knap and Doeschl-Wilson 2020; Bai and Plastow 2022). Knap and Doeschl-Wilson (2020) suggested that disease resilience can be modelled as a reaction norm of production on pathogen load, given known levels of resistance and tolerance. Epidemiological characteristics of a disease, such as the occurrence of super-spreaders, can have a strong influence on exposure of herd-mates to a pathogen (Eady *et al.* 2003). As a consequence, disease resilience of a population is a property of the group that is more than the sum of the disease resilience of its members (Doeschl-Wilson *et al.* 2021). This well developed model of disease resilience provides a basis for examining the concepts of context-specific and general resilience below.

Measuring resilience

Many of the studies of resilience described above are based on repeated measurement of variables within an individual animal across a period of time. Statistical measures of the dynamic properties of such longitudinal data have been used to quantify deviation from a prior trajectory or periodic pattern. Examples include variance, autocorrelation, skewness and periodicity (Scheibe *et al.* 1999; Nunes Marsiglio Sarout *et al.* 2018; van Dixhoorn *et al.* 2018; Berghof *et al.* 2019a; Iung *et al.* 2019; Poppe *et al.* 2020) although other statistical measures of deviation and synchronisation of periodicity have been used (Scheibe *et al.* 1999; Putz *et al.* 2019; Nguyen-Ba *et al.* 2020; Wagner *et al.* 2021). The narrative description of resilience and the statistical methods for its estimation are *normative* models of biological function. Thus, the trajectory of a performance trait, or the periodic behaviour of a variable is theorised or empirically estimated to be a smooth function (e.g. Nguyen-Ba *et al.* 2020; Ben Abdelkrim *et al.* 2021). By focusing on resilience as a desirable characteristic of the animal, conformity to a normal trajectory is valued by the scientist above deviation or change in a trajectory that may represent reprioritisation of the use of resources by the animal. In this conceptualisation, the resilient animal is understood to defend expression of a trait or biological function against environmental perturbations (Baffy and Loscalzo 2014). Is this normative model of biological function in accord with models of physiological regulation and stress? Before addressing this question, some other points on measuring resilience are noteworthy.

First, in most assessments, the baseline from which deviations are estimated for quantifying resilience is the performance trajectory of the individual animal. In idealised form, this approach measures the success of the individual in achieving its inherited and developmentally acquired potential for expression of a performance trait, and contrasts with assessment of production which is measured against performance of other individuals. Thus, whereas productivity is a measure of absolute production or production efficiency, resilience is a measure of uniformity of biological function that may be independent of the

actual level of production performance. In practical terms, resilience has been found to be a trait different from production (Elgersma *et al.* 2018) and, in dairy cows, it is negatively correlated with milk yield (higher-yielding cows have lower resilience; Poppe *et al.* 2020).

Second, an alternative approach to assessing resilience was used by Hine and colleagues (Aleri *et al.* 2019; Hine *et al.* 2019, 2021, 2022). These authors measured the strength of the immune response during the stress of routine husbandry practises such as weaning of beef calves and lambs bred and raised in a pasture-based production system. This approach measures the absolute level of performance of the immune system, termed immune competence, under stress rather than characteristics of response kinetics (Hine *et al.* 2019, 2022) and complements a large body of work on associations between immune competence and disease outcomes in livestock (for reviews, see Wilkie and Mallard 1999; Hine *et al.* 2015; Mallard *et al.* 2015; König and May 2019; Bai and Plastow 2022). Immune competence measured in dairy heifers during routine husbandry is negatively correlated with cortisol responses (Aleri *et al.* 2019) and thus immune competence may be an indicator of resilience. In support of this conclusion is the observation that protective host responses to heat stress are stronger in cows with high immune competence (Cartwright *et al.* 2021, 2022).

Third, structure and complexity within the daily organisation of behaviour has been analysed as an indicator of resilience to environmental stressors such as a barren environment in mice (Freund *et al.* 2013) or feed shortage in chickens (María *et al.* 2004). The salient feature of these studies is that behavioural complexity at the individual and the group level is reduced in stressful conditions. Loss of complexity is also a hallmark of physiological activities under stressful conditions (Asher *et al.* 2009; Baffy and Loscalzo 2014). A review of statistical methods for analysis of behavioural complexity as potential indicators of resilience is provided by Asher *et al.* (2009).

Finally, detailed accounts of methods for analysis of dynamic indicators of resilience are provided by Baffy and Loscalzo (2014), Scheffer *et al.* (2018), Scheibe *et al.* (1999), Nunes Marsiglio Sarout *et al.* (2018), Berghof *et al.* (2019*b*) and Weinans *et al.* (2021). For a critique of dynamic indicators as measures of resilience, see Knap and Doeschl-Wilson (2020). Dynamic indicators of resilience are based on resilience theory and are described as generic indicators of systemic resilience that can provide whole-of-animal indicators of the animal's state in the face of environmental perturbations (Scheffer *et al.* 2018).

Physiological regulation of trait expression

What do models of physiological regulation tell us about the trajectory of performance traits? Briefly, the development and expression of morphological and biological functions during ontogeny and later life exhibit varying degrees of robustness and plasticity in the face of environmental variation. The physiological processes supporting robustness and plasticity are respectively termed homeorhesis and allostasis. Homeorhesis describes the activity of physiological intermediaries such as neuroendocrine and peripheral tissue-derived hormones in guiding the transition of the animal to a new physiological state such as lactation, and then maintaining and buffering the state against environmental fluctuations (Waddington 1942; Bauman and Currie 1980). Homeorhesis is a whole-of-animal modulation of physiological activities in support of a physiological state or performance trajectory (for review, see Colditz 2020). The homeorhetic regulatory environment modulates sensitivity of tissues to homeostatic signals such as insulin and changes the range within which variables such as blood glucose are regulated (Bell and Bauman 1997). Homeorhesis constrains (canalises) expression of form and function along trajectories that exhibit resistance to disturbance by environmental variation. This buffering of a trajectory against environmental fluctuations is seen in many contexts in livestock including pregnancy (Greenwood *et al.* 2017) and compensatory growth (Wilson and Osbourn 1960). Nonetheless, many biological functions can adapt and exhibit plasticity in the face of environmental change and express a modified level of performance (Goldstein and Kopin 2007; Baffy and Loscalzo 2014). Physiological regulation of plasticity has been termed allostasis (Sterling and Eyer 1988; Romero *et al.* 2009; Koolhaas *et al.* 2011), although the term is also used to describe the short-term anticipatory regulation of physiological functions within their normal homeostatic range (Schulkin and Sterling 2019). As with homeorhesis, the influence of allostasis on morphology and sensitivity of tissues to homeostatic signals can change the range and response characteristics of homeostatic variables (Goldstein and Kopin 2007; Romero *et al.* 2009; Koolhaas *et al.* 2011). The rapid return to a homeorhetic trajectory of performance is likely to arise from homeostatic process operating within the homeostatic range established by homeorhetic regulation (Bauman 2000; Baffy and Loscalzo 2014; Colditz 2020; Friggens *et al.* 2021).

It is evident from the preceding discussion that homeorhesis and allostasis are abstract conceptual models of physiological processes that are used to account for phenomena of persistence or variability in trait expression and biological function in the face of environmental variation. Many biotic and abiotic factors contribute to environment variation, and environmental conditions can vary over long and short timescales. The spatial scale of environmental variation can extend from the individual animal (micro-environment) to the level of the cohort, farm, or geographic region (macro-environment; Strandberg 2009). Heritable variation in the stability of trait expression may differ between micro- and macro-environmental scales

(Madsen *et al.* 2021). Nonetheless, a degree of arbitrariness exists in drawing a distinction between robustness (macro-environmental scale) and resilience (micro-environmental scale) (Friggens *et al.* 2017, 2021). Plasticity is also a heritable trait (Strandberg 2009; Santana *et al.* 2013). Whereas resilience describes a normative pattern of trait expression, plasticity describes a deviation from this norm towards an altered (and sometimes adaptive) pattern (Baffy and Loscalzo 2014). Selection for plasticity would value flexibility over uniformity. It is noteworthy that a capacity to return to a prior pattern of performance following an environmental perturbation is described as adaptive plasticity by some authors (e.g. Nunes Marsiglio Sarout *et al.* 2018, and references therein). Is resilience a desirable characteristic to breed for? Beneficial long-term outcomes associated with resilience could provide some justification.

Consequences of resilience

A strong focus of studies on resilience has been placed on associations with subsequent health, fitness and production outcomes. Favourable associations have been identified between resilience indicators and desirable longer-term outcomes in a number of contexts. Measures of deviation in daily milk yield of dairy cows were favourably genetically correlated with better udder health, longevity of the cow within the herd, fertility, body condition score and dry-matter intake, and reduced susceptibility to ketosis (Poppe *et al.* 2020). Characteristics of the milk yield curve and behavioural activity in the first lactation were associated with longevity and reproductive performance (Adriaens *et al.* 2020). Variability in daily feed intake and feeding duration were genetically correlated with mortality and treatment rates in pigs exposed to natural disease challenge (Putz *et al.* 2019). Using a measure of the capacity of beef steer calves to mount an immune response to vaccination during the stress of weaning while confined in outdoor cattle yards, Hine *et al.* (2021) found a favourable association between high immune competence and low mortality during subsequent finishing in a commercial feedlot. Immune competence measured during the stress of yard weaning in lambs was favourably genetically correlated with the incidence of fly strike, faecal soiling of the breech (dag score), faecal worm egg count, and a composite fitness measure (Hine *et al.* 2022). Deviations from normality in average eating time, daily ear temperature dynamics and daily behavioural activity in late pregnancy were predictive of a suite of health deficits in early lactation in dairy cows (van Dixhoorn *et al.* 2018). There are many additional studies on beneficial outcomes related to resilience in livestock reported in the literature.

Gradual loss of resilience may be an intrinsic characteristic of ageing and senescence. Analysis of the dynamic characteristics of serial white blood cell counts and daily activity assessed by wearable devices in large datasets in humans reveal an association between resilience and longevity. Past an age in the mid-40s, the magnitude of deviations and duration of recovery time in both variables increased in proportion to age, which the authors interpreted as indicating physiological resilience declines with an increasing age as an intrinsic process of senescence in a manner that sets an upper limit on lifespan (Pyrkov *et al.* 2021).

The individual resilience score for dairy cows based on daily milk yield variance, shape of the lactation curve and behavioural activity, when averaged at the farm level, has been found to differ substantially among farms (Adriaens *et al.* 2020; Poppe *et al.* 2021*a*). Farms with poor resilience scores tend to have a higher proportion of cows with rumen acidosis, higher somatic cell count, lower fat content, longer calving interval, lower survival to second lactation, larger herd size, lower lactose content, and higher production (Poppe *et al.* 2021*a*). The results have illustrated the potential for resilience scores calculated at the farm level to provide a measure for benchmarking welfare performance among farms (von Keyserlingk *et al.* 2012; Colditz *et al.* 2014).

Together, these findings lend support to resilience being a desirable attribute of the animal both for its short-term benefits manifest as uniformity of daily performance and for its association with longer-term beneficial outcomes. A recurrent question raised by such favourable associations is the extent to which resilience is context-specific or is a characteristic of animals that is expressed as a general trait in the face of a diversity of environmental challenges. The question leads to a consideration of resilience as a conceptual construct.

Resilience as a conceptual construct

Behind field studies of many biological phenomena are abstract theoretical models of the relationships that exist between measured variables and underlying characteristics of the animal. These models constitute conceptual constructs that are not always able to be directly observed (Scott *et al.* 2001). Friggens *et al.* (2021) suggested that the concept of resilience in livestock is just such a multi-faceted construct and that it is obscured from direct measurement. Tools used to quantify resilience, the authors suggest, can reveal aspects of the underlying construct of resilience, while assessment of the cumulative longer-term consequences of resilience, such as health and fitness outcomes, are needed to provide external validation of the construct. This insightful observation helps establish a framework for refinement of the conceptual construct of resilience and for its implementation through

measurement tools for use in welfare assessment and for phenotyping animals for genetic analyses.

Many concepts in biology are abstract multi-faceted constructs that cannot be directly measured. To quantify the construct, proxy variables can be measured from which a value or state of the hidden or latent trait is inferred. Examples include unobservable constructs such as intelligence, personality and quality of life (Scott *et al.* 2001). Detailed methods have been established in psychometrics for developing and validating constructs, for developing measurement instruments such as scoring scales for assessing the individual, and for analysing scores. For examples of application of these methods to development of measurement instruments for assessing health-related quality of life in animals, see Reid *et al.* (2022) and personality (temperament) in animals see Carter *et al.* (2013).

An important component of a conceptual construct is the relationship that is theorised to occur between the measured variables and the underlying character or latent trait of the animal described by the construct. Several types of relationship are theorised. First, the measured variables can be indicators that reflect aspects of the underlying construct but are neither caused by nor do they causally influence the construct (Fig. 1a). Health-related quality of life is an example of this class of conceptual construct (Reid *et al.* 2022). Second, when a causal relationship is theorised to exist between the measured variables and the hidden construct, causation is theorised to take one of at least three forms, namely, (1) the measured variables cause the latent trait (Fig. 1b), (2) the measured variables are caused by the latent trait (Fig. 1c), or (3) the measured variables interact in a network that manifests the latent trait as an emergent system property of the network; the latent trait is not considered to exist as an entity that is separate from interactions among the network variables (Guyon *et al.* 2017; Fig. 1d). For a detailed account of the application of these three models to theories of emotions (appraisal, constructionist, affect-program) in humans, see Lange *et al.* (2020). In simplified terms, for the example of the emotion of fear in animals, in causal Model 1, an increase in heart
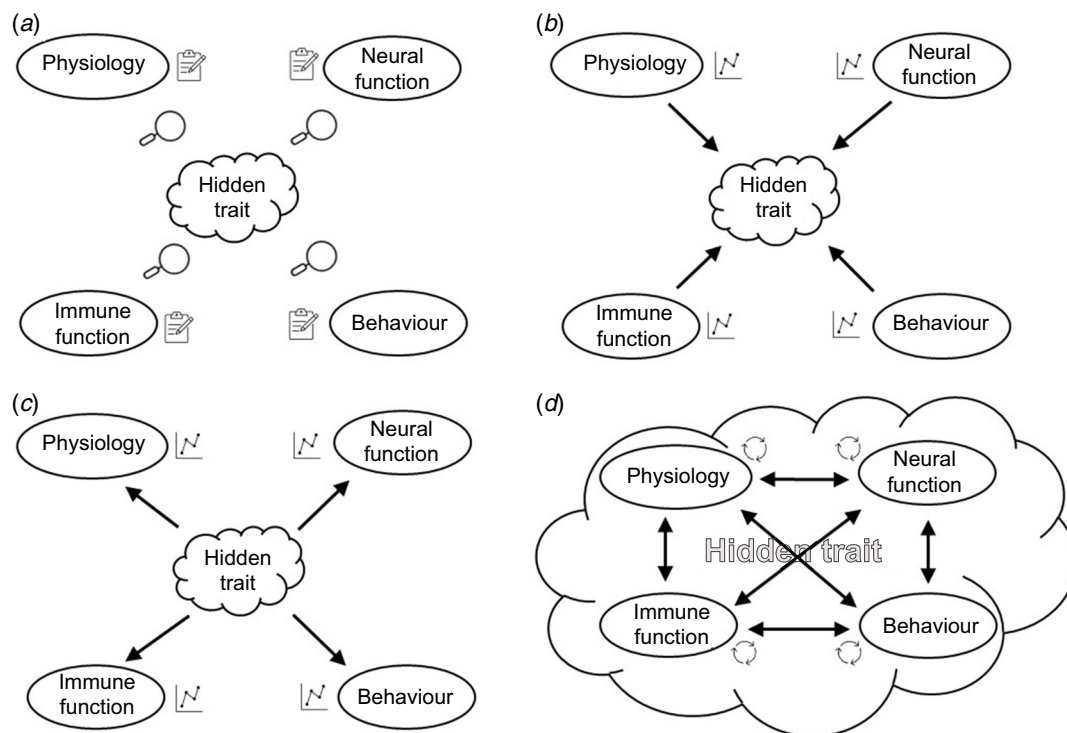

Fig. 1. The relationships between measurements or scores made of an animal and a hidden trait or conceptual construct such as fear, temperament or resilience can take a number of forms, four of which are shown here. (*a*) Scores made on the animal reveal aspects of the hidden construct but are not causally linked to the construct. (*b*–*d*) Causal links lie between the hidden construct and biological functions that can be assessed by measurement of variables in those functions. (*b*) Biological functions such as physiological, behavioural, immune and neural activities are causes of the hidden trait. (*c*) The hidden trait causes changes in biological functions such as physiological, behavioural, immune and neural activities. (*d*) The hidden trait is embedded within a network of biological functions such as physiological, behavioural, immune and neural activities and is an emergent property of the activities within the network. More complex nested hierarchies of causation occur than are represented here.

rate would be part of a suite of physiological and behavioural changes that cause occurrence of the emotion of fear. In Model 2, occurrence of the emotion of fear would cause a suite of physiological and behavioural changes including increase in heart rate. In Model 3, changes in a suite of physiological and behavioural variables occurring in a particular situation or context evince a system property within the network of interacting variables that is, in and of itself, an instance of fear (Fig. 1*d*). Network theory (Model 3) has recently been applied to animal welfare (Rowland *et al.* 2021) and resilience (Scheffer *et al.* 2018). In this view, attributes such as fear and temperament (and resilience, as discussed below) are not substantive entities that can act like an extra hand to manipulate yet other entities such as cognition, immune function, behaviour or energy metabolism. Rather, attributes such as fear and temperament are distributed properties realised through activity within subcellular, cellular, organ and whole-body processes (Baffy and Loscalzo 2014; Guyon *et al.* 2017; Scheffer *et al.* 2018; Colditz 2021).

For hidden constructs such as health-related quality of life, the *definition* of the construct is considered to be independent of the variables. Thus, scores of energy, happiness, comfort and calmness that are used in the assessment of health-related quality of life in animals reveal aspects of the construct but do not themselves define health-related quality of life (Reid *et al.* 2022; Fig. 1*a*). In contrast, where a causal relationship lies between the construct and the measured variables, the variables often provide at least a partial definition of the construct (Fayers and Hand 2002). For example, the concept of glucose homeostasis, which in broad conceptualisation is a dynamic whole-of-animal state (Baffy and Loscalzo 2014), can be operationalised by proximate measurements of blood concentrations of glucose, insulin, and glucagon (Modell *et al.* 2015). In this minimal model, glucose homeostasis is defined as the balance among the measured variables glucose, insulin and glucagon. Yet, moving beyond these initial measures, the construct can be further refined as an outcome state arising from the dynamics of expression levels of the various glucose receptor types on target tissues, intracellular enzyme kinetics, glycogen reserves, autonomic tone, liver health, pancreatic function and more (Bell and Bauman 1997). In this manner, the construct can be defined at various levels of refinement by the variables that are measured.

A further characteristic of unobservable constructs is the lack of an external gold standard against which to validate that the measured variables give a true report of the status of the hidden trait (Fayers and Hand 2002). It is a common conclusion that assessment of the welfare state of an animal lacks such an external gold standard (Scott *et al.* 2001). This statement differs from use of the term gold standard to describe a benchmark or threshold of performance against a suite of indicators that is deemed to constitute an acceptable or optimal (gold standard) level of welfare [for examples of this important and entirely valid usage of the term, see Mellor and Stafford (2001) and Sandgren *et al.* (2009)]. The relationship between the measured variables and the unobservable construct remains a theoretical model that can be iteratively refined and validated through well described procedures for construct validation (Fayers and Hand 2002; Carter *et al.* 2013). For examples of the application of methods for construct validation to human–animal relationships, see Waiblinger *et al.* (2006), and for animal personality, see Carter *et al.* (2013).

Many measurements made on animals can be validated against external gold standards. For example, measurement of milk yield of goats can be validated against volumetric or gravimetric standards, and data on daily milk yield over the course of a lactation can be used to generate an empirical model of the lactation curve of the individual animal (for an example, see Ben Abdelkrim *et al.* 2021). Complementing the empirical model can be a suite of more abstract concepts, some of which may be less accessible for direct measurement than the expressed phenotype of daily milk yield. A plausible hierarchy of progressively more abstract concepts in this example could include the propositions that (1) a performance trait, such as a lactation curve, is expressed as an unperturbed dynamic trajectory across time in an ideal environment, (2) failure of an animal to cope with environmental perturbations can compromise expression of a performance trait such as daily milk yield as an unperturbed dynamic trajectory, and (3) reiterating Broom (1996), the state of the animal as it attempts to cope with its environment is a fundamental aspect of its welfare that can be partially revealed through analysis of the trajectory of a performance trait. The hierarchy provides a transition from an empirical model of an expressed production trait that has been validated against an external standard to a hidden construct of welfare that lacks direct concordance with a gold standard.

Many of the 'big ideas' in biology such as consciousness, temperament, emotion, affective valence, fitness, homeostasis, homeorhesis, allostasis, stress, sustainability, health and welfare share with resilience this character of being multifaceted constructs that can be partially revealed from various perspectives through application of assessment tools and by measurement of proximate mechanistic processes. Such concepts often appeal to an intuitive understanding grounded in folk wisdom and are used in a manner described in semiotics as floating signifiers. One approach to constraining abstract constructs is to define the construct as being limited to the variables that are measured for its estimation as illustrated for disease resilience (e.g. Knap and Doeschl-Wilson 2020; Bai and Plastow 2022) and for homeostasis (e.g. Modell *et al.* 2015). Herein lies a paradox. The same careful definition of variables that is essential for accurate genetic evaluation of a manifest trait (Haskell *et al.* 2014) can hamper development of the underlying conceptual construct. While ongoing development, refinement and validation of the concepts and their empirical relation to

biological outcomes is of utmost importance, theoretical and empirical development can proceed simultaneously, and resolution of the conceptual construct is not a prerequisite for application of a version of the construct in practical studies (Dawkins 2021).

The diversity of hypotheses that align with the concept of stress helps illustrate this point. In a review of the literature on studies examining the role of stress in behavioural and physiological processes involved in life-history trade-offs, developmental transitions, health, and survival, Harris (2020) identified 131 hypotheses that propose a role for stress in these outcomes. While many of the hypotheses shared similarities and made similar predictions, the diversity of hypotheses illustrates a lack of harmonisation and consolidation of the concepts both at a theoretical level and when they are tested in experimental studies. Many of the hypotheses are highly cited within the animal welfare literature, yet none of the hypotheses on the role of stress in animal welfare was captured in the literature review or represented in the classification framework developed by the author. Nonetheless, the lack of conceptual clarity as to what stress is, how it operates, and the consequences of its occurrence does not diminish the central importance of the conceptualisation and measurement of stress to understanding animal welfare.

From this background, it follows that the concept of resilience is likely to be used in the literature at various degrees of conceptual abstraction and refinement. This provides a tone of caution to the search for a simple unified concept of resilience.

Personality as an analogy for resilience

What might a multi-faceted construct of resilience look like? The relationship between the different components of a multifaceted construct can be difficult to resolve. For resilience, a central question is whether there is a unitary construct that can manifest as general resilience across a diversity of environmental contexts, including infectious disease, husbandry stressors, climatic variability, social stress and so on, or whether resilience in each context is a separate trait as suggested by Llonch *et al.* (2020). Studies on defined phenotypes in defined environmental contexts such as the examples described above can provide pragmatic answers to whether context-specific resilience has utility for assessing welfare and for breeding. Nonetheless, a number of authors have suggested that a more general character of the animal may exist that can confer resilience across a diversity of environmental contexts, thereby providing a range of beneficial outcomes (e.g. Hine *et al.* 2015; Colditz and Hine 2016; Scheffer *et al.* 2018; Putz *et al.* 2019; Harlizius *et al.* 2020; Sun *et al.* 2021). The question gains importance because of potential implications for identifying

the context in which to measure the general resilience phenotype and the variables suitable for its quantification.

Personality provides an example of a multifaceted construct of importance in animal science that may help illustrate how resilience as a unitary construct may operate across multiple dimensions and contexts. All animals are considered to have a 'temperament' or 'personality'. In abstract form, temperament/personality is often described as having five aspects, namely, exploration, activity, aggressiveness, sociability, and boldness, which are shown through persistent patterns of behaviour that are repeated across contexts or across time within a context (Réale *et al.* 2007; Carter *et al.* 2013; Finkemeier *et al.* 2018). Importantly, the relative level of expression of each aspect of temperament can differ consistently among individuals, and covaries with physiological, immunological and performance differences among individuals (Careau and Garland 2012). The relationships between temperament and physiological and immunological functions and performance have been interpreted to support a conceptual model of temperament as an attribute of the animal that manifests in, and is operationally defined through, behaviour alone, with the underlying latent variable temperament exerting a causal influence on other functions such as immune and metabolic activities. A large number of tests such as flight speed in cattle have been developed to measure aspects of temperament (Burrow 1997). Genetic and phenotypic associations of a measured trait such as flight speed with productivity, meat quality, health and reproductive performance can be utilised in animal management and breeding programs (Haskell *et al.* 2014). In contrast to assessment of one aspect of temperament *via* a single test, performance of animals in a suite of tests such as judgement bias and attention bias tests in cattle can be analysed to estimate the relative contribution of various aspects of temperament to the behaviours measured in each test (Kremer *et al.* 2021). In this example, the authors concluded that differences among individuals in activity, fearfulness (the opposite of boldness) and sociability modulated their activity in the tests. Such studies contribute to the ongoing refinement of the general concept of temperament and methods for its assessment, and enable application of the general concept and the specific tests to questions, such as the influence of affective state on performance in the tests and, conversely, the utility of the tests to measure affective state when performance is conditioned on temperament scores (Kremer *et al.* 2021). Ongoing interpretation of the relationships among behaviours, physiology, immune function and performance support refinement of the causal model of temperament to the concept of temperament as a distributed network property embedded in physiological, immunological and performance functions as well as in behaviour (Colditz 2021), a model no doubt requiring further refinement. The distributed/embedded network model suggests that

measurement of the underlying temperament trait might be improved by measurements made on each dimension rather than by measurements solely of behaviour, a proposition supported by studies on body temperature and blood lactate as predictors of temperament in cattle (Williams *et al.* 2019). The example of temperament illustrates that the core concept of resilience could exhibit various aspects that individuals consistently express to varying extents in different contexts such as disease, social and climatic challenges, and that measurement of multiple aspects could improve triangulation of the underlying conceptual construct. This conceptual model of resilience aligns closely with that proposed by Friggens *et al.* (2021). A challenge for advancing this field of research is to tolerate ambiguity in the conceptual construct, while specific measures of 'resilience' are refined through empirical studies.

Implications for health and welfare

Most indicators of resilience have been found to have low to moderate heritability in the livestock species studied and to be favourably associated with health outcomes (Berghof *et al.* 2019*b*). As a consequence, resilience indicators are attracting considerable interest for inclusion in animal breeding goals (Berghof *et al.* 2019*b*). Nonetheless, the biological links between a capacity to be minimally affected by short-term fluctuations in the environment, as evidenced by performance trajectories, biorhythms and functional complexity, and longer-term outcomes such as longevity, reproductive performance and incidence of disease are not well characterised. Protracted exposure to many types of stressor is recognised to generate negative affective states and to be associated with increased mortality and poor health outcomes in humans and animals (Walker *et al.* 2012). Thus, affective states may provide a plausible link between resilience and the outcomes associated with resilience. There is increasing emphasis in studies of animal welfare of the need to not only minimise harms but to also enable the animal to achieve positive welfare outcomes (Yeates and Main 2008; Mellor 2015; Lawrence *et al.* 2019; Mattiello *et al.* 2019; Fig. 2). Does resilience merely minimise harms or is resilience an aspect of positive welfare? If resilience provides a measure of positive welfare, does it do so as a proxy for positive affect, or does resilience represent an aspect of positive welfare not captured solely by positive affect?

The nature of positive welfare and methods for its assessment are topics under rapid advancement (reviewed by Yeates and Main 2008; Mellor 2015, 2016; Lawrence *et al.* 2019; Mattiello *et al.* 2019; Rault *et al.* 2020; Keeling *et al.* 2021). Lawrence *et al.* (2019) suggested that the concept of positive welfare includes (1) positive affective states, (2) engagement with the environment in a manner that provides positive affective experiences, (3) quality of
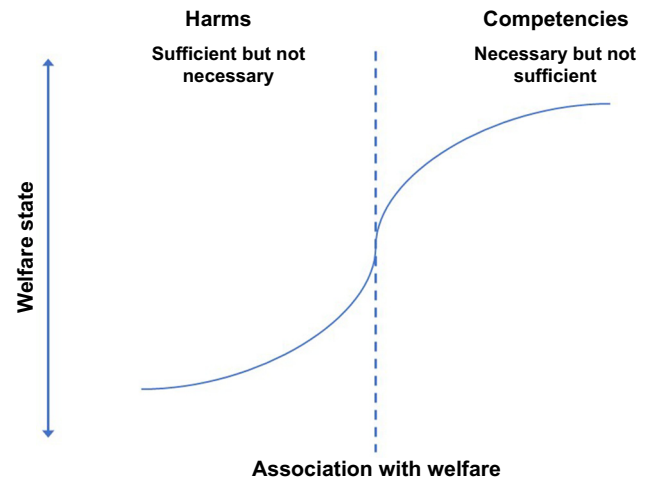
Fig. 2. The welfare state of an animal falls on a continuum from poor to positive. The point of inflection between positive and poor welfare does not occur at a fixed sum of harms versus competences. Rather it can occur at any point where the influence of any single factor becomes sufficient for it to constitute a harm and reduce welfare, although any specific individual harm is not necessary for a state of poor welfare to exist. Positive welfare depends on the occurrence of multiple 'competencies to thrive' that are each necessary, but are not individually sufficient, for positive welfare to occur. Characterisation and assessment of competencies to thrive as indicators of eudaimonic and hedonic wellbeing requires further research.

life arising from the balance of positive and negative states, and (4) happiness across the whole of the animal's life. This view aligns positive welfare with opportunities for achieving and experiencing hedonic wellbeing. Nonetheless, in philosophical and empirical studies, two strands of wellbeing have been recognised, hedonic and eudaimonic (Ryff *et al.* 2004; Nordenfelt 2006, 2011; Fredrickson 2016; Rault *et al.* 2020; Williams 2021). Eudaimonia describes the capacity of the animal to express agency, function well, and fulfil biological potential, which together enable the animal to display mastery of its environment (Ryff *et al.* 2004; Fredrickson 2016; Williams 2021). This has been termed 'doing' by Lawrence *et al.* (2019). From a human perspective, the eudaimonic dimension of wellbeing can be captured by the epigram 'I function well, therefore I flourish.' It differs from the hedonic perspective of wellbeing, which for humans can be characterised as 'I feel well, therefore I am well.' In the style of Lawrence *et al.* (2019), hedonic wellbeing can be abbreviated to 'feeling' (e.g. Robbins *et al.* 2018; Duncan 2020). A third strand centred on social wellbeing has also been described in some frameworks of human and animal wellbeing (Williams 2021) which can be termed 'interacting'.

Rault *et al.* (2020) and Williams (2021) emphasised the importance of developing indicators of eudaimonia to advance studies on positive animal welfare. Some preliminary lines of evidence for potential physical indicators come from

studies in humans and rodents. Self-report of indicators of eudaimonic wellbeing in humans are associated with a gene transcription pattern in leukocytes that accompanies strong antibody and antiviral defence (Cole *et al.* 2015). The transcription pattern is shifted to a proinflammatory profile, termed the conserved transcriptional response to adversity, by early life adversity and by a range of stressors, and is associated with poor health outcomes (Fredrickson *et al.* 2015). Surprisingly, the (undesirable) pro-inflammatory profile is also positively associated with indicators of hedonic wellbeing (Fredrickson 2016). The same effect of stressors on leukocyte gene transcription is observed in rodents and rhesus monkeys (Cole 2019). In accord with these findings, in independent studies in humans, eudaimonic wellbeing was associated with *lower* concentrations of daily salivary cortisol, pro-inflammatory cytokines, metabolic markers of cardiovascular risk, and longer-duration REM sleep; a pattern not seen for indicators of hedonic wellbeing (Ryff *et al.* 2004). Contrary results have also been reported (reviewed by Williams 2021). Despite divergence in biomarkers between eudaimonic and hedonic wellbeing, these two (or three) aspects of wellbeing are closely intertwined in humans and the authors interpret their findings as pointing to benefits associated with indicators of eudaimonia rather than harms accompanying indicators of hedonia (Fredrickson 2016).

Another line of evidence supporting the role of normalcy of biological functioning in generating positive wellbeing is provided by the hypothalamic–pituitary–adrenal (HPA) axis. In all mammals examined, including sheep (Fulkerson 1978), cortisol production exhibits circadian and ultradian patterns that are influenced by genetic background, sex hormones, neonatal epigenetic programming, environmental stressors and age (Russell *et al.* 2015). The circadian pattern of HPA activity modulates mood and metabolic, immunoregulatory, and cognitive activities in anticipation of the activity cycles of the animal (Russell *et al.* 2015; Kalafatakis *et al.* 2021). Disruption of the circadian and ultradian patterns increases susceptibility to a variety of physical and psychological stressors, and animals (rats and humans) with more pronounced circadian and ultradian patterns exhibit greater resilience to stressors (Spiga and Lightman 2020). Thus, circadian and ultradian rhythms increase resilience during the period of heightened risk of exposure to stressors that accompanies activity. These studies on periodicity of HPA axis function lend support to findings on measures of periodicity of other physiological and behavioural variables as indicators of resilience and eudaimonic wellbeing (Scheibe *et al.* 1999; Nunes Marsiglio Sarout *et al.* 2018; van Dixhoorn *et al.* 2018; Sun *et al.* 2021; Wagner *et al.* 2021).

This background supports the proposition that uniformity of performance trajectories and periodicity of physiological cycles provide signs of mastery by the individual of its personal environment. These measures of resilience may

indicate not only that the animal is coping with the potential harms posed by its environment but is also expressing a positive state of eudaimonic wellbeing that enables it to thrive. It is important to note that these measures are indicators of systemic or whole-of-animal resilience (Scheffer *et al.* 2018). The analytical methods assess the 'structure' within biological functions rather than the mechanistic interactions among components that underlie particular functions. Thus, where resilience is indicated as low, the measures may lack specificity for identifying the welfare domain [nutrition, environment, health, behaviour, or affective mental state (Mellor and Beausoleil 2015)] or welfare criterion (Veissier *et al.* 2009) in which provisions or biological functions are deficient (Fig. 3). Thus, dynamic indicators of resilience, and the eudaimonic state inferred from the indicators, represent a higher-order level of welfare assessment than domain-specific indicators of hedonic positive welfare currently under development, for example, as described for ruminants by Mattiello *et al.* (2019) and Keeling *et al.* (2021).

Competence

A framework for interpreting the beneficial effects of biological functions in support of eudaimonic wellbeing is provided by the concept of competence. Waddington (1957) developed the idea of competence to describe the acquisition of responsiveness to developmental cues by cells and organs during ontogeny. The concept of competence is widely used in biology and has been extended from Waddington's limited application in embryogenesis to describe emergence of biological functions on both phylogenetic and ontogenetic time scales. It is the development of functions such as immunity, social skills and coping skills during the lifespan of the individual that is of importance in the current context. Such functionalities often exhibit phases of rapid maturation during periods of heightened sensitivity to the inductive effects of environmental stimuli, although acquisition of competence can continue outside sensitive periods and continue into adult life (Mellor 2019; Colditz 2020; Lyons and Schatzberg 2020). Following its early historical description in sense organs (Hubel and Wiesel 1970), the concept of competence has been extended to describe development of functionalities in reproduction, immunity (Miller 1963), physiology (Timiras 1996) and psychology (White 1959; Hintze and Yee 2021; Williams 2021). For example, play can be understood to contribute to the development of competence in long-term social, muscle motor and kinaesthetic (proprioceptive) capabilities that contribute to agency as well as providing short-term hedonic rewards (Spinka *et al.* 2001; Špinka and Wemelsfelder 2011). Competence also underpins the notion of hormesis (López-Otín and Kroemer 2021), that is, the induction of resilience to stressors by
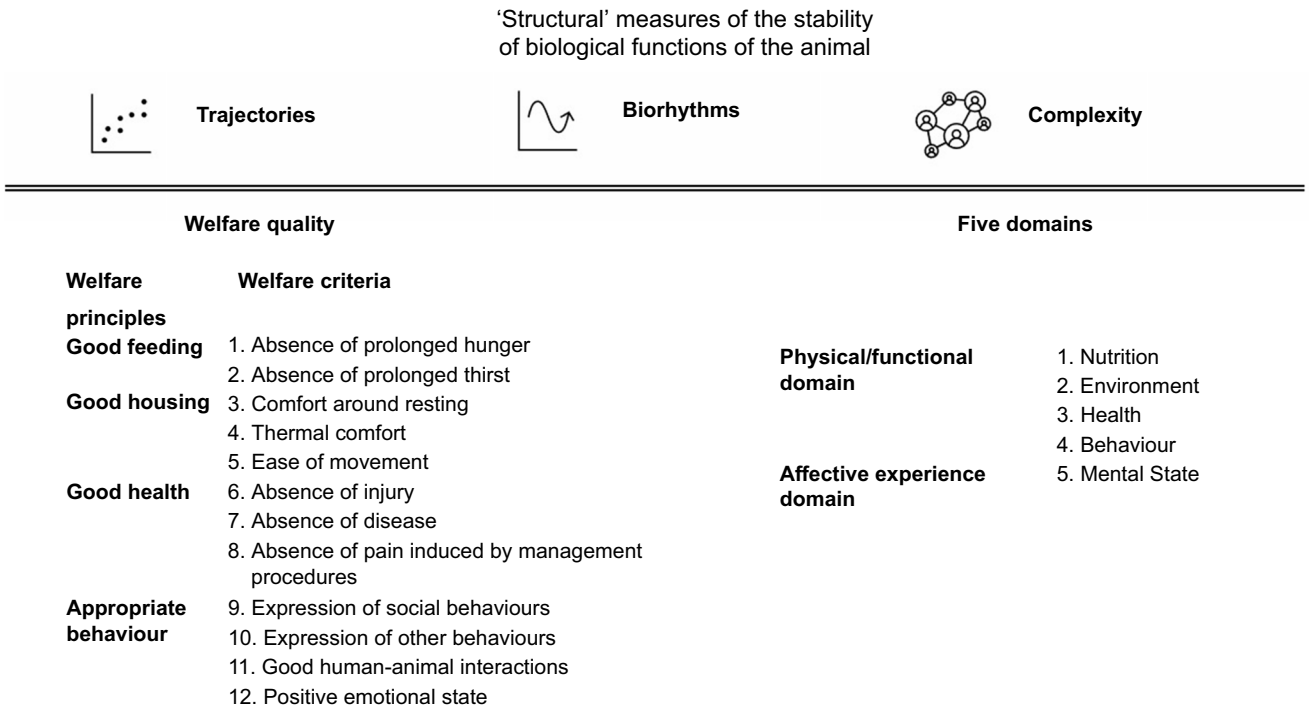
'Structural' measures of the stability
of biological functions of the animal

Trajectories   Biorhythms   Complexity

Welfare quality

Welfare principles	Welfare criteria
Good feeding	1. Absence of prolonged hunger
	2. Absence of prolonged thirst
Good housing	3. Comfort around resting
	4. Thermal comfort
	5. Ease of movement
Good health	6. Absence of injury
	7. Absence of disease
	8. Absence of pain induced by management procedures
Appropriate behaviour	9. Expression of social behaviours
	10. Expression of other behaviours
	11. Good human-animal interactions
	12. Positive emotional state

Five domains

Physical/functional domain	1. Nutrition
	2. Environment
	3. Health
	4. Behaviour
Affective experience domain	5. Mental State

Fig. 3. Indicators of resilience based on trajectories, biorhythms and complexity can provide integrated indicators of the eudaimonic dimension of positive affective experience. However, the indicators can lack specificity to identify in which welfare criterion of the Welfare Quality model derived from the Five Freedoms (Veissier *et al.* 2009) or welfare domain of the Five Domains model (Mellor and Beausoleil 2015) deficiencies in biological functioning occur when resilience is low. In the tripartite model of animal wellbeing (Williams 2021), complexity of social interactions (Asher *et al.* 2009) might provide an indicator of social wellbeing.

low-dose exposure in an appropriate context during developmental stages (Lyons and Schatzberg 2020). Acquired resilience or 'learning to cope' has been studied as a competence in humans, monkeys and mice that can be acquired through exposure to conducive experiences (Lyons and Schatzberg 2020). Although competencies are developmentally acquired through experience, genetic variation exists in the capacity of the animal to develop competencies, as seen, for example, in the heritable variation in immune competence in beef cattle (Reverter *et al.* 2021). A critical feature of the acquisition of competencies is the role of appropriate environmental conditions. This role of engagement with enriching environments in development and ongoing realisation of competencies underpins the 'provision' statements in the Five Freedoms and the Five Domains frameworks (Mellor 2015, 2016). Thus, the role of competencies in realising physiological, cognitive and affective potential of the animal anchors them firmly within the concept of positive welfare.

Positive health

Studies on indicators of eudaimonia in humans and other animals have led to the development of the concept of positive health (Ryff *et al.* 2004; López-Otín and Kroemer 2021). In this view, 'health is an active process that enables an organism to adapt to fluctuations in its intrinsic and extrinsic environments to maintain health or recover to a healthy state after disease occurs' (Ayres 2020). This view recognises a distinction between defence mechanisms such as those centred on immune functions that antagonise infections, and pro-active physiological, behavioural and psychological mechanisms that promote health (Ayres 2020; Medzhitov 2021; Fig. 4). Thus, positive health is more than the absence of ill-health. Defence mechanisms are typically associated with a catabolic state, whereas the pro-active mechanisms supporting positive health are associated with an anabolic state (Ye and Medzhitov 2019). The concept of health as a continuum was highly influential in the development of the concept of animal welfare as a continuum from poor to good (Broom 1996). Yet, the concept of health, like other abstract concepts discussed in this review, attracts diverse opinions as to its character and the indicators that signal its occurrence (Lerner 2020). This ambiguity is illustrated by a review of the use of the concept in 500 textbooks of veterinary medicine and pathology. Gunnarsson (2006) suggested the definitions of veterinary health used in these textbooks fall into five categories: (1) normality; (2) biological function; (3) homeostasis; (4) physical and psychological wellbeing;
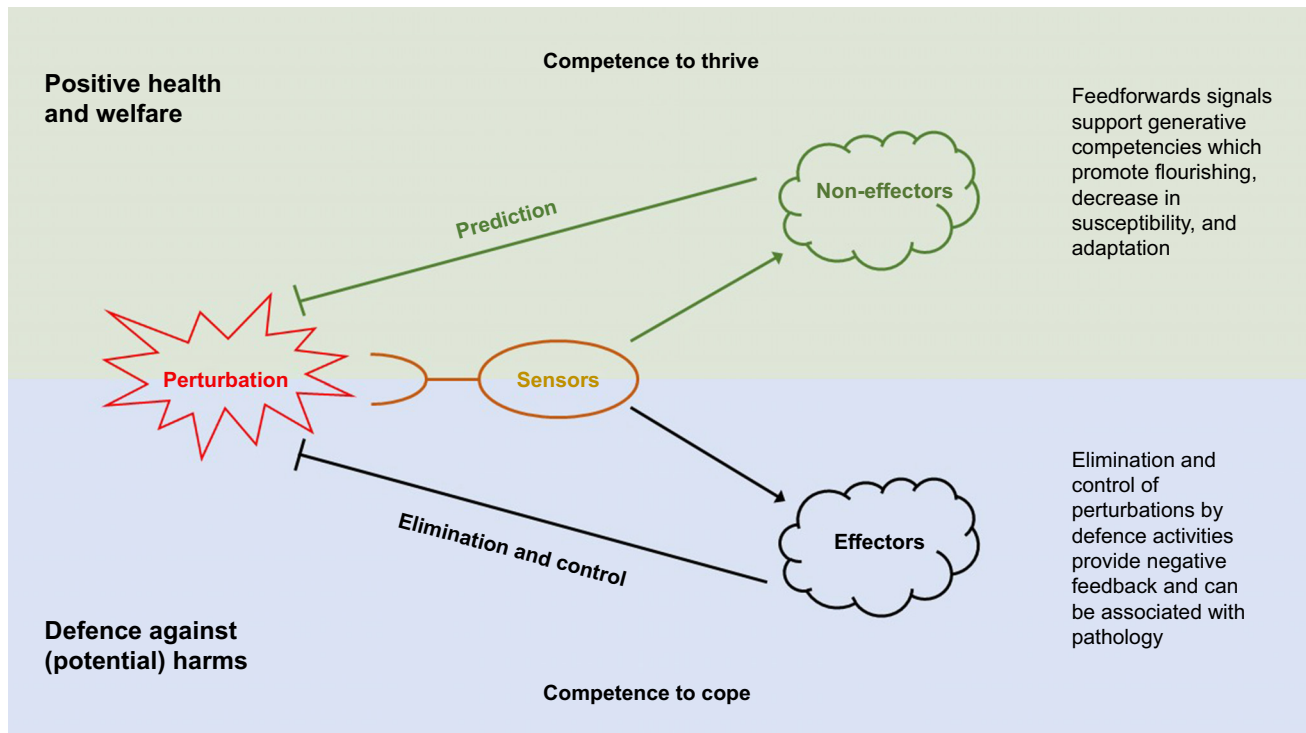
Fig. 4. Perturbations in the structure, function or regulation of tissues, processes and activities of the animal are detected by sensors that stimulate effector defence processes that provide negative feedback on the causes of the perturbation by its elimination or control and underpin 'competence to cope'. Signals from sensors provide feedforward stimuli to non-effector tissues promoting generative competencies that support thriving, loss of susceptibility, and adaptation to the causes of perturbation. Together these feedforward signals promote 'competence to thrive' that generates a eudaimonic state of positive health and positive welfare.

and (5) productivity including reproduction. It is noteworthy that 92% of the surveyed texts relied on the reader's intuitive understanding of the concepts of health and disease. Studies on resilience and regulation of host defence (e.g. Lyons and Schatzberg 2020; López-Otín and Kroemer 2021; Medzhitov 2021) have illustrated the opportunity for further development of resilience measures as indicators of positive health, and positive health as an aspect of positive welfare. The mechanistic differences between host defence and positive health identified by Ayres (2020), Lyons and Schatzberg (2020), López-Otín and Kroemer (2021) and Medzhitov (2021) support a distinction between elimination and control of harms through 'competence to cope' and prediction and avoidance of harms in support of flourishing of the animal through 'competence to thrive' (Fig. 4).

A continuum of affective experience

Central to the conventional concept of positive welfare as described above is positive hedonic affective experience. A framework that links eudaimonia and hedonia as aspects of positive welfare is provided by considering the continuum of affective experience. Animals are thought to continuously

exist in an affective state described as a psychological space with dimensions of hedonic valence and arousal (Russell 2003; Mendl *et al.* 2010; Kremer *et al.* 2020; Fig. 5). Valence describes attractiveness or aversiveness and arousal describes the level of psychological activation of affective experience. Both valence and arousal influence autonomic nervous system functions and are hence associated with changes in physiological arousal (Satpute *et al.* 2019). In humans, self-report provides the foundation for assessment of affective states; however, as self-report is not available for non-human animals (or prelingual infants), physiological and behavioural changes can provide proxies for affective states (Russell 2003; von Borell *et al.* 2007; Hemsworth *et al.* 2015). In the network model, physiological and behavioural changes are attributes of an affective state but are not alone sufficient to describe the state. Transient affective states that change over short time-frames (moments to minutes) are described as emotions, which typically have an object focus on events in the internal and external environments of the animal (Russell 2003; Mendl *et al.* 2010; Kremer *et al.* 2020). In contrast to emotions, affective experiences that dwell over periods from hours to days generate free-floating moods that are less focussed on events and more closely aligned with an accumulation of recent affective experience (Russell 2003; Mendl *et al.* 2010;
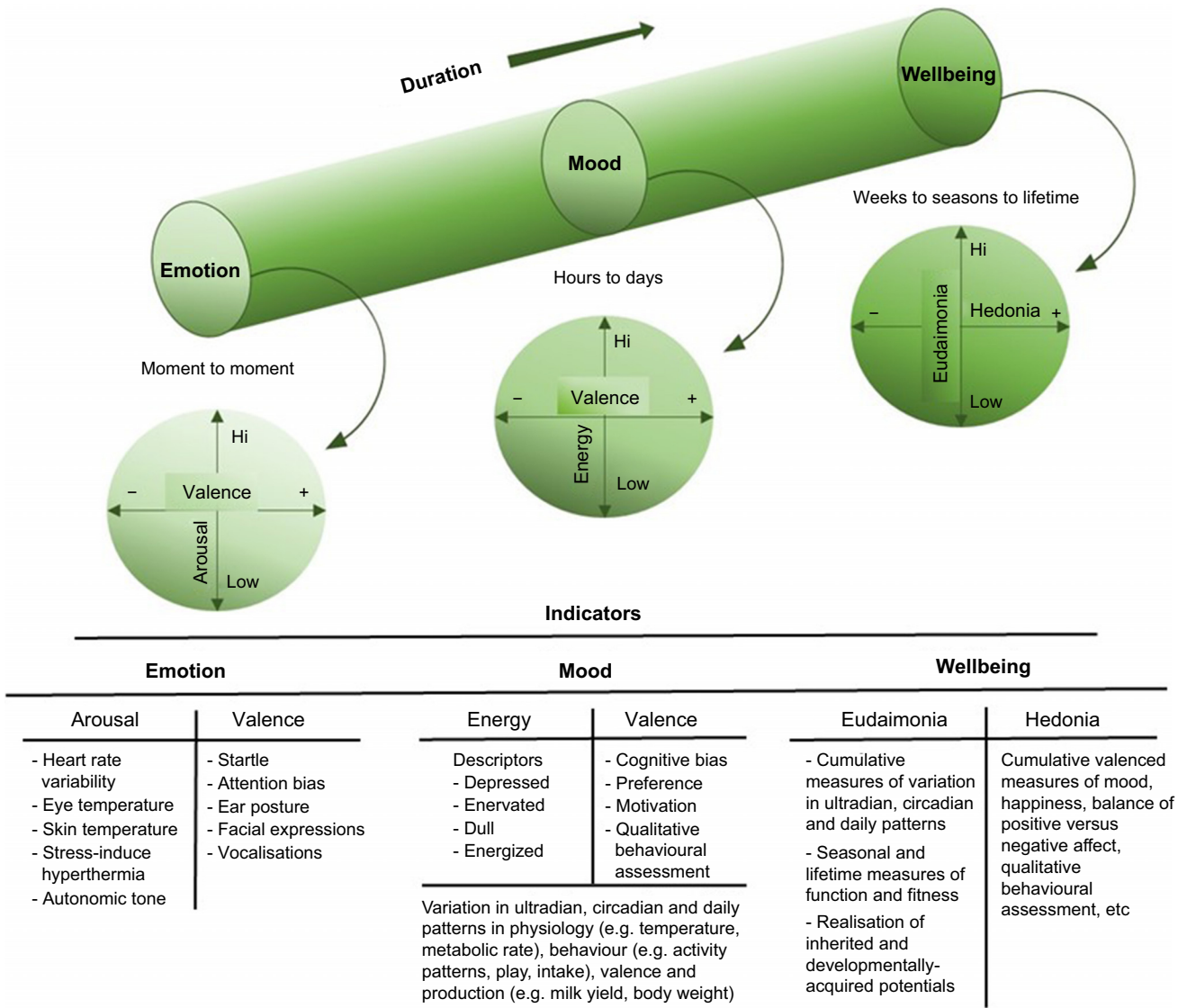
Fig. 5. The animal occupies an affective space with dimensions of hedonic valence and psychological arousal. Position in affective space can vary over time-frames that change from moment to moment (emotions) or hours to days (moods). It is suggested here that wellbeing represents a persistence of affective experience over periods that last from weeks to seasons to whole of life. The eudaimonic and hedonic dimensions of wellbeing may be aspects of affective valence and arousal. As animals are unable to self-report their affective experiences, valence and arousal of emotions and moods can be assessed through physiological, behavioural and cognitive proxies. Most measures of resilience that have been developed examine physiological functions associated with the time-frame of moods. Eudaimonia may represent the accumulation of short-term physiological functions as well as functions of the animal such as longevity and fitness that manifest only over longer time-frames. Resilience measures developed address the eudaimonic dimension but are largely lacking for the hedonic dimension of wellbeing. Resilience measures of hedonic wellbeing are plausible, such as periodicity of positively valenced mood.

Kremer *et al.* 2020). Like emotions, moods are described as representing the position of the animal in psychological affective space with dimensions of valence and energy (arousal; Russell 2003; Mendl *et al.* 2010; Kremer *et al.* 2020; Fig. 5). The physiological manifestation of the energy of moods is captured in descriptors such as dull, depressed, active, and energised and the valenced dimension by behaviours such as sickness behaviour (negatively valenced; Johnson 2002) and

play (positively valenced; Špinka 2012). It is evident that sickness behaviour is accompanied by a low-energy state and play by a high-energy state. The co-expression of energy and valence in the psychological state associated with play and sickness behaviour illustrates the important point that the position of the animal in affective space cannot be described solely by proxy measures of either arousal (energy) or valence (Russell 2003; Mendl *et al.* 2010; Kremer *et al.* 2020).

It is suggested here that the two dimensions of affective experience may dwell over the longer time-frames of seasons, years and the whole life of the animal to manifest as eudaimonic and hedonic wellbeing (Fig. 5). The persistence of eudaimonic and hedonic states over long intervals of time is well recognised in humans (e.g. Ryff *et al.* 2021). In this model, neither eudaimonia nor hedonia can alone provide a complete description of the psychological affective experience of wellbeing. The model is consistent with the proposition that an animal can experience simultaneously divergent levels of eudaimonic and hedonic wellbeing (Williams 2021). For example, an aged cow may have poor eudaimonic wellbeing from the privations of advancing age while experiencing good hedonic wellbeing associated with suckling, grooming, and being groomed by her calf. This re-iterates the observation that good health and positively valenced affective experience can occur independently and are not synonymous (Duncan and Dawkins 1983).

The physical aspects of eudaimonic function that have been captured by measures of resilience have largely focussed on variability of performance in the time-frame of days to seasons. Whole-of-life measures to extend this time-frame may be provided by cumulative measures of health, longevity, evolutionary fitness, and the success of the animal in achieving its inherited and developmentally acquired capacity for performance (Fig. 5). Measures of the hedonic valence of affective experience that dwell over time-frames from days to whole-of-life would complement eudaimonic measures in describing the whole-of-life welfare of the animal. Cumulative scores of affect balance and affective hedonic happiness have been proposed as measures to assess such long-term hedonic wellbeing in animals (Mellor 2016; Webb *et al.* 2019; Kremer *et al.* 2020; Keeling *et al.* 2021).

In the transition from transient emotions to longer-lasting moods, the character of affect is thought to change from an object focus to a diffuse experience (Russell 2003; Mendl *et al.* 2010). Accompanying this shift in focus is a transition from acute alterations in autonomic nervous system functions that manifest as arousal to longer-lasting changes in kinetic energy that manifest as strength of motivations and behavioural activity levels (Mendl *et al.* 2010; Kremer *et al.* 2020). These transitions in system functions between emotions and mood highlight an important question whether there are further transitions in system functions that become manifest only in the psychological states of long-term eudaimonic and hedonic wellbeing. In this scenario, wellbeing (and welfare) would be more than the sum of biological functions and valenced experience measured on ultradian, circadian and daily time scales, and would require measures of whole-of-animal properties that are not expressed on the time scales of moments and days. In the Domains Model of welfare assessment, the mental state arising from positive or negative affective engagement is proposed to provide an integrated sum of internal states

and external circumstances (Mellor and Beausoleil 2015). Indicators of positive affective experience under development for assessment of positive welfare have largely focused on behaviours that are indicative of positively valenced states (Lawrence *et al.* 2019; Mattiello *et al.* 2019; Keeling *et al.* 2021). It is suggested here that when affective experience is parsed into eudaimonic and hedonic dimensions that resilience indicators can be understood to provide integrated measures of eudaimonic healthy physical functioning that extend the suite of indicators available for the assessment of positive welfare. This can help satisfy the recognised need for tools to assess eudaimonic wellbeing (Lawrence *et al.* 2019; Rault *et al.* 2020; Williams 2021).

Conclusions

The capacity of an animal to exhibit minimal disturbance to its normal patterns of physiological, behavioural and performance activities in the face of variations in its micro-environment provides signs of its competence to thrive and to fulfil its inherited and developmentally acquired potential. Animals express consistent individual differences from their conspecifics in performance trajectories (e.g. growth rate), biorhythms (e.g. chronotypes; Refinetti *et al.* 2016) and complexity of social interactions (e.g. dominance). Longitudinal data enable estimation of deviation from the pattern that is normal for the individual (Buller *et al.* 2020), whereas cross-sectional data necessitate estimation of deviation from the pattern that is normal for the population. The micro-environment, which is also termed the 'non-shared environment' in co-housed animals (Freund *et al.* 2013), describes the individual perspective an animal has of its conditions. In this respect, measures of resilience address the need in animal welfare science to assess the conditions the individual animal experiences from its own perspective (Dawkins 2006). Differences among individuals in the occurrence of deviations across time while they are being managed within a shared macro-environment confirm that resilience can measure the individual animal's experience of its non-shared micro-environment, and that differences among individuals can occur in the absence of any overt macro-environmental disturbance (Nunes Marsiglio Sarout *et al.* 2018; Garcia-Baccino *et al.* 2021). Resilience assessed by these parameters of individual normalcy may provide new indicators of health, biological functioning and the state of the individual animal as it attempts to cope with its environment. The continuous monitoring of animals and their environment by sensor technologies has come to be termed precision livestock farming (Buller *et al.* 2020). The analytic strategies being developed to assess resilience when combined with genomic predictions of individual animal performance should enable the development of a

'personalised medicine' approach to precision welfare assessment of the individual animal.

Although the conceptual construct of resilience may be hidden from direct measurement, pragmatic measures based on physiological, behavioural and performance variables expressed in the routine production environment and during periods of husbandry induce stress, such as weaning, change of diet or social regrouping may inform refinement of the conceptual construct. This pragmatic approach aligns with Dawkins' suggestion that it is not necessary to unravel the role of consciousness in affect and emotion so as to establish the valence of animal experience through behavioural assessment of 'what animals want' (Dawkins 2021). Biological costs to the animal of resilience may be less than the costs of adaptation (Strandberg 2009; Ayres 2020; Douhard *et al.* 2021; Garland *et al.* 2022), and deserve further research.

It is well recognised that harms and deprivations are sufficient to reduce welfare of an animal in any prior degree of good welfare (Broom 1986; Fig. 2), and that to sustain good welfare requires not only the minimisation of harms but also the cumulative combination of what can be termed 'competencies to thrive' based on healthy functioning across behavioural, immunological, physiological, cognitive and affective domains (Mellor 2016). An important question for development of indicators of positive welfare is whether these competencies represent a eudaimonic dimension of positive welfare or only indirectly contribute to positive welfare through the provision of opportunities for positive hedonic affective experience (Hemsworth *et al.* 2015; Mellor 2016; Weary and Robbins 2019). Both modes of influence seem likely, as suggested by theory (Williams 2021), by empirical studies on folk intuitions of good welfare (Robbins *et al.* 2018) and as summarised in Fig. 5. Thus, it is suggested that health and proper biological functioning, which have long been recognised as important aspects of welfare, not only indicate the absence of harms but can also indicate a eudaimonic state of positive welfare. Resilience may provide a sensitive physical indicator of eudaimonia. In this view, positive welfare entails both eudaimonic and hedonic aspects of wellbeing, neither of which is alone sufficient to describe the state of positive welfare, nor alone sufficient to maximise positive welfare.

The utility of measures of trajectories, biorhythms, and functional complexity as indictors of the current state of the animal, as predictors of future outcomes or as phenotypes for genetic evaluation does not depend on the validity of the constructs of resilience, competence, positive health or eudaimonia presented in this review. Rather, their utility lies within empirical relationships established through field studies. Further refinement of the constructs and their relationships with animal measures should help improve assessment of animal welfare and our understanding of the biology of 'doing'. It is noteworthy that numerous studies in humans have reported a circadian periodicity in positive mood that is disrupted in states of physical and psychological dysfunction (Kalafatakis *et al.* 2021, and references therein). It is highly likely that similar periodicity occurs in animals. If biosensors for detecting physiological and behavioural proxies of positively valenced mood can be developed for animals, then the parameters of normativity used to assess resilience may provide simple measures of hedonic wellbeing that can help advance understanding of the biology of 'feeling' in farm animals.

The opportunity to breed animals for resilience does not diminish the importance of minimising the risk of harms by good management of animals of appropriate genetic background in well designed environments. Cumulative scores of resilience may provide a method for quantifying one aspect of the whole-of-life welfare of the individual (Nunes Marsiglio Sarout *et al.* 2018; Friggens *et al.* 2021; Poppe *et al.* 2021*a*), as well as provide a tool for benchmarking welfare performance among farms. Further work on development of these measures of resilience and their application to welfare assessment is warranted. These new measures enabled by sensor-derived longitudinal data offer the opportunity to detect the impact of 'periods of acute, but transitory, physical or mental suffering' on the animal that Brambell (1965) recognised provide a limitation to use of 'growth and condition' as indicators of welfare.

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