frontiers | Frontiers in Animal Science

TYPE Review
PUBLISHED 29 June 2023
DOI 10.3389/fanim.2023.1101957

OPEN ACCESS

EDITED BY
Ruth Catriona Newberry,
Norwegian University of Life Sciences, Norway

REVIEWED BY
Maria José Hötzel,
Federal University of Santa Catarina, Brazil
Manja Zupan Šemrov,
University of Ljubljana, Slovenia

*CORRESPONDENCE
Donald M. Broom
dmb16@cam.ac.uk

RECEIVED 18 November 2022
ACCEPTED 09 June 2023
PUBLISHED 29 June 2023

CITATION
Broom DM (2023) Can positive welfare counterbalance negative and can net welfare be assessed? *Front. Anim. Sci.* 4:1101957. doi: 10.3389/fanim.2023.1101957

Can positive welfare counterbalance negative and can net welfare be assessed?

Donald M. Broom*

Department of Veterinary Medicine and St Catharine's College, University of Cambridge, Cambridge, United Kingdom

The absence of poor welfare is important for welfare to be good, but measures of good welfare are of great value in welfare assessment. Assessors of the welfare of individuals need to know the overall balance of good and poor. Direct behavioural measures and measures of physiology, such as oxytocin concentration, together with experimental studies of motivation, help in evaluating whether positive or negative components of welfare are prevailing in a given situation. Studies of humans and other animal species are described. While there are few detailed comprehensive studies measuring positive and negative welfare in the same individuals, examples are given of overall measurements of consequences when there could be positive and negative effects. Measures of net welfare, when positive and negative components have been resolved, are described. It is concluded that good welfare can often counterbalance poor welfare but does not do so in all circumstances.

KEYWORDS

welfare, motivation, feelings, pleasure, suffering, pain, fear

1 Introduction: negative and positive welfare

For all animals, welfare is the state of the individual as regards its attempts to cope with its environment and involves a wide range of coping mechanisms. Not only are basic cellular and physiological mechanisms and many defences against disease the same in humans and non-humans, but complex brain mechanisms, such as many cognitive functions and feelings, can be identified in sentient wild and domestic animals, not only in humans (Broom, 1986; Broom, 1998; Lawrence et al., 2019; Webb et al., 2019; Tarazona et al., 2020; Bornmann et al., 2021; Zentall, 2021; Broom, 2022a). A feeling is a brain construct, involving at least perceptual awareness, that is associated with a life-regulating system, is recognizable by the individual when it recurs, and may change behaviour or act as a reinforcer in learning (Broom, 1998). A feeling that can be described physiologically is referred to as an emotion (Boissy et al., 2007; Broom, 2007). Hence, the concepts of "emotion" and "feeling" overlap in meaning, and an emotion is a physiologically describable component of a feeling, characterised by electrical and neurochemical activity in particular regions of the brain, autonomic nervous system activity, hormone

release, and peripheral consequences, including behaviour (Broom, 2022b, see also Rolls, 2005; Broom, 2014). Sentience means having the capacity to have feelings. This capacity includes having the awareness and, in many situations, the cognitive ability necessary to have feelings (Broom, 2014; Broom, 2022b). The positive end of the welfare scale is often called good welfare, while the negative end is called poor welfare. Welfare science involves identifying and assessing positive and negative welfare and the balance of what is positive or negative for the individual. The assessment methods identify how good/positive or how poor/negative each component of the welfare is. Consideration of this issue should always take account of a function of intensity and duration, i.e., the magnitude of good or poor welfare (Broom, 2001; Broom, 2022a). All of these questions are exactly the same for human or non-human animals, as there is only one biology.

When an individual of any species is said to have good welfare, this usually means that there are high levels of pleasure, happiness, contentment, control of interactions with the environment, or possibilities for exploiting abilities. Positive welfare is likely to be the normal situation in much of life for wild animals (Browning and Veit, 2023). Positive feelings are associated with good control and are often a part of a positive reinforcement system, just as poor welfare is associated with various negative reinforcers. The close links between positive feelings and actions that help in achieving effective control of life are emphasised in the concept of positive affective engagement (Mellor, 2015; Lawrence et al., 2019). The term 'affect' refers to a valenced experience involving positive or negative moods, emotions or feelings (Crump et al., 2018). While individual positive feelings may help in controlling life, a net overall positive in the various coping systems over a longer period will have greater effect. Individuals living in an environment that meets more of their needs may differ from those living in a more barren environment. For example, young domestic chicks prefer to spend time close to a chick-sized moving object and, when living with this, are less disturbed by a startling stimulus than chicks living without such a preferred object (Broom, 1969).

A question often asked is whether good welfare is solely the absence of poor welfare or whether it is the extent of contentment or pleasure. A review by Boissy et al. (2007) concludes that it is a serious mistake to assume that good welfare is merely the absence of poor welfare. Most animal welfare scientists would say that identifying good welfare involves assessing the extent of both indications of the absence of poor welfare and those of positive welfare (e.g., Würbel, 2009; Broom, 2014). Questions asked here are whether or not good welfare can compensate for poor welfare, how much compensation can occur, and how any compensation and the overall balance, i.e., net welfare (Browning and Veit, 2023), can be measured. A further important ethical question is "what is positive enough?" The answer to this will differ according to the subject individual and the evaluator. Philosophers have written extensively about which humans and which non-human individuals deserve or should be given the best welfare, but the general ethical question will not be discussed further here.

In a study comparing fMRI measurements of humans in positive and negative situations, Lindquist et al. (2016) begin by stating that all human cultures have a concept of valence and that this integrates the positive and the negative. It is pointed out that even human infants of a few days of age differentiate between positive and negative and react to the balance between them. Lindquist et al. acknowledge that arousal level affects the outcomes of any balancing and conclude from their analysis that, once the balance has been evaluated, it "is flexibly implemented across instances by a set of valence-general limbic and paralimbic brain regions". They do not find evidence for independent brain systems for the positive and negative. It seems very likely that the mechanisms underlying the valence of feelings in humans would also occur in other species. An acute pain or a sudden frightening sound would be negative for humans or chickens, and pleasure associated with the taste of good food or with the achievement of solving a problem would be positive. There is variation among individuals because welfare is affected in humans and other animals by differences in sensory capacities, as well as the coping mechanisms being used and the timescale. An evaluation of the balance of positive and negative at a certain time might be changed rapidly or slowly by events that alter components of welfare.

The viewpoint that positive and negative can be integrated might seem to contrast with the emphasis of Diener and Emmons (1984) on the independence of positive and negative affect. They found that memory of positive and negative affect depends on time frame and on how emotional the individual is at time of remembering. However, the effects of different sets of factors on different kinds of affect, and on recall of events and their impact, does not mean that integration of affect cannot occur. A welfare assessment system should reflect basic considerations concerning the breadth of the term and the goal of the welfare assessment. It is widely agreed that welfare assessment in an individual animal should encompass as much as possible of the range from very positive to very negative (Fraser, 2008; Fraser et al., 2013; Broom, 2022a). In this article, references are made to many examples of welfare assessment, using a wide range of methodologies. The methods are not described in detail, so the original text or review of methodologies (e.g., Fraser, 2008; Broom and Johnson, 2019; Broom, 2022a) should be consulted for more detail.

2 Identifying and balancing good and poor welfare

2.1 Motivation and decisions

Much of life for every individual animal — a human, a rabbit, or a minnow — involves taking decisions in order to cope with the world around that individual by minimising poor welfare and maximising good welfare. The timescale may necessitate short-term or long-term trade-offs. The opportunities will be constrained by general environmental aspects, so options for a free-living human, rabbit, or minnow will be somewhat different from those for a captive human, rabbit, or minnow. Hence, scientific measures of the welfare of individuals assess degree of negative and degree of positive welfare, and an understanding of motivation is of great importance in welfare assessment. The motivational systems that

function in humans and other animals have evolved and exist now because they are adaptive (Broom, 1981; Mendl and Paul, 2020; Broom, 2022a). Most of the strong positive preferences of animals are for resources or actions that benefit them: that is, that help them to survive, breed successfully, and have good welfare. During development, individuals will have acquired further information that helps them to take decisions that lead to benefits. Although motivational systems are complex, it is helpful to think of motivation as including incentives or goals (Toates, 2002). Kringelbach and Berridge (2015) suggest that actions aimed at increasing the likelihood of feeling pleasure are ubiquitous in sentient animals. Incentives encourage the occurrence of much behaviour (Dickinson and Balleine, 1995; Dickinson and Balleine, 2002; Berridge, 2018; Perez and Dickinson, 2020). One consequence of this for welfare research (Duncan, 1978; Dawkins, 1983; Dawkins, 1990; Duncan, 1992; Broom and Johnson, 2019) is that the assessment of motivational strength during tests of preference is useful in any attempt by humans to ensure that poor welfare is avoided and good welfare is maximised. Although most strong positive preferences relate to something wholly positive, there can be preferences for drugs that result in some short-term pleasure but longer-term negativity, or for high-risk activities in humans and in non-human species. Similarly, the extreme level of avoidance shown towards a running insect or small mammal may not be justified by the average degree of danger from such animals. Extreme preferences should be investigated by studying the consequences when the preferred resource is obtained or the preferred action is taken. For the assessor of welfare, as for the individual studied, the balancing of positive and negative is necessary, either continuously or at intervals. Some examples of this are now considered.

2.2 Welfare measures and balancing positive and negative

Many measures of good or poor welfare have to be considered when planning how to assess the welfare of an individual, and single measures sometimes do not indicate the extent of how good or how poor welfare is. For example, facial expression can indicate pain or pleasure (Lansade et al., 2018; McLennan et al., 2019b), but can be simulated by individuals and can convey false information in humans and other species (Barrett et al., 2019). Collections of measures and further information about the state of the individual can improve accuracy of evaluation. However, individuals may be deceived about their own welfare. A diseased individual may be unaware of pathology that limits its ability to cope with environmental impacts (Fraser 2008; Broom and Johnson, 2019; Broom, 2022a). In a largely philosophical discussion of whether suffering dominates enjoyment, Groff and Ng (2019) point out that welfare measures may sometimes indicate what the individual studied perceives to be their welfare at that time, rather than their actual welfare.

Some components of coping systems may act independently, but there will also be summating effects and integration of component effects. For example, rats may suppress pain responses when predators are present, and a sheep with pain from foot-rot may continue to show behavioural evidence of pain if it is with a familiar flock feeding calmly, but may suppress any such behaviour if potential predators are present (Sorge et al., 2014; McLennan and Mahmoud, 2019a; McLennan et al., 2019b, Broom personal observation). Such summation by an individual must often involve compensation between negative and positive in the determination of the outcome. Negative experiences often lead to avoidance behaviour, while positive experiences tend to lead to approach. A positive balance may be demonstrated using simple behavioural measures. However, preference measures are most valuable if the strength of preference is assessed. Measurement of the amount of work that an individual will invest in the approach or avoidance often, but not always, gives good information about the extent of net negative or positive welfare.

Welfare measures for an individual can indicate good welfare, poor welfare, or net welfare, i.e., the balance between good and poor. At any particular time, there may be net positive or net negative welfare, so resolving the negative and the positive is important for the assessor. Biological mechanisms result in individuals having needs, and the fulfilment of these is associated with good welfare. When all needs are met, the individual's behaviour and physiology are more likely to indicate normality and positive welfare to animal welfare scientists. As a consequence, normal behaviour can be used as an indicator of good welfare and lack of normal behaviour can indicate poor welfare. However, care is needed when using readily visible indicators of welfare. Human and non-human individuals often attempt to appear normal when they are disturbed in some way. Displaying signs of pain or fear to a predator or revealing to another individual that a communication is perceived in a very negative way could have fatal or other negative consequences, so such signs are often concealed. Behaviour judged to be abnormal behaviour by human observers is often associated with a welfare problem, both when it is adaptive and when it is maladaptive (Broom, 2006; Broom, 2014). Hence, one of the ways of identifying and quantifying good welfare is to observe a wide range of normal behaviour. Especially important is behaviour that can be demonstrated to be positively preferred, taking account of the strategies and inefficiencies of functioning that may be evident when normal behaviour is occurring (Broom, 2022a). Welfare is usually better if all positively preferred behaviours can be shown than if some are prevented. Both what is liked, in that the consequences are greater numbers of happy actions and fewer unhappy actions, and what is wanted, in terms of what is often chosen when the opportunity arises, are important to individuals (Yeates and Main, 2008). If positive preferences have been fulfilled and negative preferences avoided, the welfare of the animal should be good, but if that which elicits negative preference predominates, net welfare is poor. Much information about the welfare of humans and non-humans is obtained in this way (Broom, 2014). Several motivational tests, such as state-specific conditioning and judgement bias, can provide useful information about the extent to which welfare is positive or negative (Mendl and Paul, 2004; Lagisz et al., 2020; Mendl and Paul, 2020). Judgement bias is the influence of affect on judgement (Broom, 2022a). Typically, subjects are trained to react differently to two stimuli that elicit relatively positive- and negative-valence outcomes. Responses to subsequent

presentations of intermediate "probe" stimuli indicate whether subjects judge them more positively (optimistic responses) or negatively (pessimistic responses). The result of a judgement bias test can indicate a net positive or net negative state in an individual (Crump et al., 2018; Broom, 2022a).

Physiological measures can directly indicate good or poor welfare. A wide range of measures examining body fluids (measuring adrenal hormones, proteins, and other indicators of tissue damage), emergency response, and other negative impacts on individuals can enable assessment of how poor welfare is (Broom and Johnson, 1993; Fraser, 2008; Broom and Johnson, 2019; Broom, 2022a). Pleasure is often associated with certain kinds of measurable brain activity and behaviour (Broom and Zanella, 2004) that may be reflected by elevated oxytocin levels in blood. Seeing positive images can increase magnetic resonance imaging (fMRI) activity on one side of the frontal area of the cerebral cortex. Phillips et al. (1998) describe a set of brain regions in which they observed activity when pictures of happy faces were seen but not during neutral or sad situations. Rewarding experiences, and positive feelings associated with these when they occur over long periods, can affect the hippocampus with consequences that are measurable *via* either MRI measures or post-mortem measures of previous brain function (Poirier et al., 2019). Oxytocin is produced in circumstances where there are clear signs of positive feelings, for example when a female mammal is nursing her young. Oxytocin is associated with the let-down of milk, but additionally leads to a feeling of pleasure (Chen and Sato, 2017). It is synthesised in the paraventricular nucleus (PVN) of the hypothalamus and in the supraoptic nucleus and binds to receptors that regulate HPA axis activity. Oxytocin is associated with parental care, emotional understanding of others, social support, inter-individual trust (Feldman et al., 2007; Ross and Young, 2009; Meyer-Lindenberg et al., 2011), and positive judgement bias in both dogs and humans (Kis et al., 2015). Oxytocin increase is associated with ACTH (adrenocorticotrophic hormone) and glucocorticoid decrease, lymphocyte proliferation, brain GABA (gamma-amino butyric acid) increase, and cardiac vagal tone increase (Carter and Altemus, 1997; Parker et al., 2005; Smith and Wang, 2012; Cardoso et al., 2014). Oxytocin can modulate emotional responses controlled by the amygdala, anterior cingulate cortex, lateral septum, ventral tegmentum, and nucleus accumbens (Tost et al., 2015). The effects of oxytocin in suppressing glucocorticoid production lead to experimental possibilities for physiological evaluation of the balance of affect when there is good welfare for one reason and poor welfare for another. However, it is not justifiable to state that oxytocin is the basis for all social behaviour (Leng et al., 2022). For example, maternal defence (Bosch et al., 2005; Bosch, 2013) may be associated with anxiety, so the effects of oxytocin may not all be positive for welfare. Change in cardiac vagal tone is another physiological measure that has been used as an indicator of good welfare. Gygax et al. (2013) described the relationships between pre-frontal cortex activity, sympatho-vagal reaction, locomotion, and behaviour indicating anticipation in rewarded and frustrated goats. Some of these physiological and behavioural measures can last for a short time and indicate brief periods of poor or good welfare. Anticipatory physiology or behaviour may indicate good or poor welfare according to what is anticipated, and the positive and negative are normally easy to distinguish.

Several behavioural measures provide some information about the balance between good and poor welfare. Prolonged stereotypies, self-mutilation, and other depressed behaviour indicate long-term difficulties in coping and hence a high magnitude of poor net welfare (Broom, 2001; Broom, 2022a). Positive experiences may not have sufficient impact to counteract the negativity. In other circumstances, there may be positive, measurable effects that compensate for anything that is negative (Lawrence et al., 2018). A net positive balance between factors with a negative impact and reward systems can be indicated by anticipatory behaviour when a reward is imminent (Spruijt et al., 2001). For example, positive-oriented anticipatory behaviour has been found to occur when rats knew from previous experience that they were about to be transferred from a barren cage to an enriched cage or to one where there would be sexual contact (van der Harst et al., 2003). Some forms of anticipatory behaviour are definable as play. Play occurs in a wide range of vertebrate and invertebrate animals (Held and Špinka, 2011; Pruitt et al., 2012; Kuba et al., 2014) and usually indicates good welfare, as it occurs in situations where welfare is good and is generally suppressed when welfare is poor (Boissy et al., 2007; Ahloy-Dallaire et al., 2018). While most of the behaviour that might be categorised as play is likely to indicate that welfare is good, some intellectual play is not readily identified by observers and some behaviour is not unambiguously play (Broom, 2014).

People who are very familiar with a domestic animal species sometimes have considerable ability to evaluate welfare. They are often making observations that are similar to those used in quantitative studies by welfare scientists. Wemelsfelder (2007) advocates the use of such human abilities in 'qualitative behavioural assessment'. This can be a useful way of assessing the balance between good and poor welfare, but can be subject to error or observer bias (Keeling, 2009; Bokkers et al., 2012; Andreasen et al., 2013), so should never be used in the absence of other welfare measurements (Muri et al., 2019; Broom, 2022a).

Many experimental studies have assessed the extent to which subjects will tolerate a negative experience in order to obtain a positive experience. Every prey species that ventures into a dangerous open space where food might be found is doing this. The assessment of risks and benefits is a key ability in life for all sentient animals (Broom, 2014). Laboratory rats have been found to be willing to move down a freezing cold pathway in order to access a preferred food source, even with other palatable food available (Cabanac and Johnson, 1983). It would seem that, in the pursuit of pleasure, considerable discomfort is tolerated (Broom and Johnson, 2019). However, having to take such decisions can be disturbing and can have sufficiently negative effects to be called stressful. Human children may risk parental reprimand in order to take a food item. In some situations, and in many species, a quantifiable risk of pain may be incurred in order to obtain a food reward. A risk of potential pain can be easier to tolerate than a risk of fear. The pain risk is more likely to be predictably limited, whereas the potential cost of some fear is death.

Fish have high levels of cognitive ability (Salwiczek et al., 2012; Broom, 2014). Studies of the responses of fish to having been caught on a hook and then released (Thorstad et al., 2003) show that further capture on a hook is avoided to a greater extent by salmon in cases of increased playing time, increased number of runs during the angling event, hooking in the throat, bleeding at the hook wound, increased handling time, or increased air exposure. Some fish are less likely to be caught on a hook if they have observed other fish being caught (Lovén Wallerius et al., 2020), but other fish allow themselves to be caught more than once (Beukema, 1970), perhaps because food is difficult to find. There can be trade-offs between predicted pain and predicted positive experience. Proximity to an individual conspecific, allogrooming, tactile stimulation, and heightened shoaling behaviour have been used as indicators of positive experience in fish (Fife-Cook and Franks, 2019). Context is important in interpretation of heightened shoaling behaviour because similar responses can be exhibited when fish are fearful.

Positive experience is normally associated with approach, but may be avoided because of highly predictable risks of negative events. A pig may refrain from approaching food because of the risk of attack by another stronger and hence dangerous pig (Mendl et al., 2010). The welfare of the fearful pig would be relatively poor but not easy to assess unless the negative state were reflected in behavioural or physiological changes.

3 Taking account of all welfare indicators

The aggregation of welfare indicators by welfare scientists into an operational welfare system is described as a process in which indicators are evaluated and re-evaluated step by step for their independent welfare relevance, marginal information value, and suitability for use in practical studies. The aggregation that is considered here is that for a set of welfare measures for a single individual. This aggregation may be repeated for each of a set of individuals. Sandøe et al. (2019) call this intra-individual aggregation and point out that this is much more likely to produce valid and usable results than inter-individual aggregation where different measures may have been taken for different individuals. Sandøe et al. also explain that, as also stated in this article, careful scientific interpretation of welfare measures must be undertaken before any derived figures can be combined. Relevant indicators for assessing the welfare of an individual can be aggregated into a protocol and this protocol evaluated in terms of relevance as a welfare assessment system (Rousing et al., 2001). Some possibilities for combining positive and negative components and a discussion of procedures and models that have been proposed to aggregate multicriteria evaluations are presented by Grabisch et al. (2008).

When there is a negative experience, this could be counteracted by a positive experience. Do people who have experienced a bereavement feel better after eating well or after sexual activity? The scientific evaluation of welfare in such a situation would have to disentangle the subject's view of what they think that they should feel, or what they say that they feel, and what they actually feel. If what they feel varies over time, so that there are short-term and longer-term effects, welfare will vary. A horse may return to a suboptimal stall because food is available there, or because humans encourage them to return or punish them for not doing so, or because they are conforming with what a group of horses do. The motivation is complex and may require much observation, experimentation, and analysis to disentangle. The question of whether or not good welfare is counterbalancing poor welfare is sometimes difficult to answer because detailed comprehensive studies investigating all aspects of this, by measuring the positive and the negative in the same individuals, are lacking. Only those studies where objective and careful measurement has been used, rather than any subjective assumption about the state of the individual, should be considered. Nicol et al. (2009) used a wide range of behavioural and physiological indicators of good and poor welfare in hens. They were able to evaluate some of the interactions between the positive and the negative and the net effects on the birds. In another comparison measuring indicators of positive and negative welfare in the same individuals, Rayner et al. (2020) found that slow-growing broiler chickens had a higher proportion of positive welfare indicators and a lower proportion of negative welfare indicators than fast-growing broilers. In the cases of other studies, different studies have to be compared to obtain such information, so the conclusions may be somewhat less reliable. However, it is clear from some approach/avoidance studies, judgement bias studies, physiological studies, and multi-measure studies that the effects of positive stimuli can often compensate to some degree for those of negative stimuli, but that they do not do so in all circumstances.

4 Conclusions

1. There are many measures of good and poor welfare, some of which are associated with positive or negative feelings and reinforcers. Some are direct measures of behaviour or physiology and some provide information about motivational state.
2. In evaluating welfare, some measures provide information about both good and poor welfare while others quantify only positive or only negative aspects.
3. There are several ways to identify a net positive or net negative effect where factors causing both negative and positive effects are present.
4. Assessing risks and benefits of actions and situations is important in the life strategies of a range of sentient animals.
5. Humans, other mammals, and other sentient animals such as fish may tolerate a negative experience in order to increase the chances of having a positive experience. and

a positive experience may be sufficient to overcome an existing negative experience, resulting in net good welfare.
6. Good welfare can counterbalance poor welfare but does not do so in all circumstances.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Ahloy-Dallaire, J., Espinosa, J., and Mason, G. (2018). Play and optimal welfare: does play indicate the presence of positive affective states? *Behav. Process.* 156, 3–15. doi: 10.1016/j.beproc.2017.11.011

Andreasen, S. N., Wemelsfelder, F., Sandøe, P., and Forkman, B. (2013). The correlation of qualitative behavioral assessments with welfare quality protocol outcomes in on-farm welfare assessment of dairy cattle. *Appl. Anim. Behav. Sci.* 143, 9–17. doi: 10.1016/j.applanim.2012.11.013

Barrett, L. F., Adolphs, R., Marsella, S., Martinez, A. M., and Pollak, S. D. (2019). Emotional expressions reconsidered: challenges to inferring emotion from human facial movements. *Psychol. Sci. Publ Interest* 20, 1–68. doi: 10.1177/1529100619832930

Berridge, K. C. (2018). Evolving concepts of emotion and motivation. *Front. Psychol.* 9. doi: 10.3389/fpsyg.2018.01647

Beukema, J. J. (1970). Acquired hook-avoidance in the pike *Esox lucius* l. fished with artificial and natural baits. *J. Fish Biol.* 2, 155–160. doi: 10.1111/j.1095-8649.1970.tb03268.x

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., et al. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiol. Behav.* 92, 375–397. doi: 10.1016/j.physbeh.2007.02.003

Bokkers, E. A. M., de Vries, M., Antonissen, I. C. M. A., and de Boer, I. J. M. (2012). Inter-and intra-observer reliability of experienced and inexperienced observers for the qualitative behaviour assessment in dairy cattle. *Anim. Welfare* 21, 307–318. doi: 10.7120/09627286.21.3.307

Bornmann, T., Randle, H., and Williams, J. (2021). Investigating equestrians' perceptions of horse happiness: an exploratory study. *J. Eq. Vet. Sci.* 104, 103697. doi: 10.1016/j.jevs.2021.103697

Bosch, O. J. (2013). Maternal aggression in rodents: brain oxytocin and vasopressin mediate pup defence. *Phil. Trans. R. Soc B* 368 (1631), 20130085. doi: 10.1098/rstb.2013.0085

Bosch, O. J., Meddle, S. L., Beiderbeck, D. I., Douglas, A. J., and Neumann, I. D. (2005). Brain oxytocin correlates with maternal aggression: link to anxiety. *J. Neurosci.* 25, 6807–6815. doi: 10.1523/JNEUROSCI.1342-05.2005

Broom, D. M. (1969). Effects of visual complexity during rearing on chicks' reactions to environmental change. *Anim. Behav.* 17, 773–780. doi: 10.1016/S0003-3472(69)80025-4

Broom, D. M. (1981). *Biology of behaviour* (Cambridge UK: Cambridge University Press).

Broom, D. M. (1986). Indicators of poor welfare. *Brit. Vet. J.* 142, 524–526. doi: 10.1016/0007-1935(86)90109-0

Broom, D. M. (1998). Welfare, stress and the evolution of feelings. *Adv. Study Behav.* 27, 371–403. doi: 10.1016/S0065-3454(08)60369-1

Broom, D. M. (2001). "Coping, stress and welfare," in *Coping with challenge: welfare in animals including humans*. Ed. D. M. Broom (Berlin: Dahlem University Press), 1–9.

Broom, D. M. (2006). Adaptation. *Berl. Münch. Tierärztl. Wochenschr.* 119, 1–6.

Broom, D. M. (2007). Cognitive ability and sentience: which aquatic animals should be protected? *Dis. Aquat. Organisms* 75, 99–108. doi: 10.3354/dao075099

Broom, D. M. (2014). *Sentience and animal welfare* (Wallingford, UK: CABI), 200.

Broom, D. M. (2022a). *Broom and fraser's domestic animal behaviour and welfare, 6th edn* (Wallingford, UK: CABI), p.545. doi: 10.1079/9/9781789249835.0001

Broom, D. M. (2022b). Concepts and interrelationships of awareness, consciousness, sentience and welfare. *J. Consciousness Stud.* 29, 129–149. doi: 10.53765/20512201.29.3.129

Broom, D. M., and Johnson, K. G. (1993). *Stress and animal welfare* (London: Chapman and Hall).

Broom, D. M., and Johnson, K. G. (2019). *Stress and animal welfare: key issues in the biology of humans and other animals, 2nd edn* (Cham, Switzerland: Springer Nature), p 230.

Broom, D. M., and Zanella, A. J. (2004). Brain measures which tell us about animal welfare. *Anim. Welfare* 13, S41–S45. doi: 10.1017/S0962728600014366

Browning, H., and Veit, W. (2023). Positive wild animal welfare. *Biol. Philos.* 38 (2), 14. doi: 10.1007/s10539-023-09901-5

Cabanac, M., and Johnson, K. G. (1983). Palatability and cold exposure in rats. *Physiol. Behav.* 31, 249–253. doi: 10.1016/0031-9384(83)90128-2

Cardoso, C., Kingdon, D., and Ellenbogen, M. A. (2014). A meta-analytic review of the impact of intranasal oxytocin administration on cortisol concentrations during laboratory tasks: moderation by method and mental health. *Psychoneuroendocrinology* 49, 161–170. doi: 10.1016/j.psyneuen.2014.07.014

Carter, C. S., and Altemus, M. (1997). Integrative functions of lactational hormones in social behavior and stress management. *Annls N Y Acad. Sci.* 807, 164–174. doi: 10.1111/j.1749-6632.1997.tb51918.x

Chen, S., and Sato, S. (2017). Role of oxytocin in improving the welfare of farm animals–a review. *Asian-Austral. J. Anim. Sci.* 30, 449. doi: 10.5713/ajas.15.1058

Crump, A., Arnott, G., and Bethell, E. J. (2018). Affect-driven attention biases as animal welfare indicators: review and methods. *Animals* 8, 136. doi: 10.3390/ani8080136

Dawkins, M. (1983). Battery hens name their price: consumer demand theory and the measurement of animal needs. *Anim. Behav.* 31, 1195–1205. doi: 10.1016/S0003-3472(83)80026-8

Dawkins, M. S. (1990). From an animal's point of view: motivation, fitness and animal welfare. *Behav. Brain Sci.* 13, 1–31. doi: 10.1017/S0140525X00077104

Dickinson, A., and Balleine, B. (1995). Motivational control of instrumental action. *Curr. Dir. Psychol. Sci.* 4, 162–167. doi: 10.1111/1467-8721.ep11512272

Dickinson, A., and Balleine, B. (2002). "The role of learning in the operation of motivational systems," in *Stevens handbook of experimental psychology*. Eds. H. Pashler and R. Gallistel (New York: John Wiley), 497–533.

Diener, E., and Emmons, R. A. (1984). The independence of positive and negative affect *J. Personality Soc. Psychol*, 47 1105–1117. doi: 10.1037/0022-3514.47.5.1105

Duncan, I. J. H. (1978). The interpretation of preference tests in animal behaviour. *Appl. Anim. Ethol.* 4, 197–200. doi: 10.1016/0304-3762(78)90086-X

Duncan, I. J. H. (1992). Measuring preferences and the strength of preferences. *Poult. Sci.* 71, 658–663. doi: 10.3382/ps.0710658

Feldman, R., Weller, A., Zagoory-Sharon, O., and Levine, A. (2007). Evidence for a neuroendocrinological foundation of human affiliation: plasma oxytocin levels across pregnancy and the postpartum period predict mother-infant bonding. *Psychol. Sci.* 18, 965–970. doi: 10.1111/j.1467-9280.2007.02010.x

Fife-Cook, I., and Franks, B. (2019). Positive welfare for fishes: rationale and areas for future study. *Fishes* 4 (2), 31. doi: 10.3390/fishes4020031

Fraser, D. (2008). *Understanding animal welfare: the science in its cultural context* (Chichester, UK: Wiley Blackwell).

Fraser, D., Duncan, I. J. H., Edwards, S. A., Grandin, T., Gregory, N. G., Guyonnet, V., et al. (2013). General principles for the welfare of animals in production systems: the underlying science and its application. *Vet. J.* 198, 19–27. doi: 10.1016/j.tvjl.2013.06.028

Grabisch, M., Greco, S., and Pirlot, M. (2008). Bipolar and bivariate models in multicriteria decision analysis: descriptive and constructive approaches. *Int. J. Intelligent Syst.* 23, 930–969. doi: 10.1002/int.20301

Groff, Z., and Ng, Y. K. (2019). Does suffering dominate enjoyment in the animal kingdom? an update to welfare biology. *Biol. Philosophy* 34, 1–16. doi: 10.1007/bf00852469

Gygax, L., Reefmann, N., Wolf, W., and Langbein, J. (2013). Pre-frontal cortex activity, sympatho-vagal reaction and behaviour distinguish between situations of feed reward and frustration in dwarf goats. *Behav. Brain Res.* 239, 104–114. doi: 10.1016/j.bbr.2012.10.052

Held, S. D., and Špinka, M. (2011). Animal play and animal welfare. *Anim. Behav.* 81, 891–899. doi: 10.1016/j.anbehav.2011.01.007

L. Keeling (Ed.) (2009). "An overview of the development of the welfare quality® assessment systems," in *Welfare quality reports no. 12* (Cardiff, UK: European Commission and Cardiff University).

Kis, A., Hernaídi, A., Kanizsaír, O., Gaícsi, M., and Topaíl, J. (2015). Oxytocin induces positive expectations about ambivalent stimuli (cognitive bias) in dogs. *Horm. Behav.* 69, 1–7. doi: 10.1016/j.yhbeh.2014.12.004

Kringelbach, M. L., and Berridge, K. C. (2015). "Motivation and pleasure in the brain," in *The psychology of desire*. Ed. W. Hofman and L.F. Nordgren (New York: The Guildford Press), 129–145.

Kuba, M. J., Gutnick, T., and Burghardt, G. M. (2014). "Learning from play in octopus," in *Cephalopod cognition*. Eds. A.-S. Darmaillacq, L. Dickel and J. Mather (Cambridge: Cambridge University Press), 57–67.

Lagisz, M., Zidar, J., Nakagawa, S., Neville, V., Sorato, E., Paul, E. S., et al. (2020). Optimism, pessimism and judgement bias in animals: a systematic review and meta-analysis. *Neurosci. Biobehav. Rev.* 118, 3–17. doi: 10.1016/j.neubiorev.2020.0701

Lansade, L., Nowak, R., Lainé, A. L., Leterrier, C., Bonneau, C., Parias, C., et al. (2018). Facial expression and oxytocin as possible markers of positive emotions in horses. *Sci. Rep.* 8, 14680. doi: 10.1038/s41598-018-32993-z

Lawrence, A. B., Newberry, R. C., and Špinka, M. (2018). "Positive welfare: what does it add to the debate over pig welfare?," in *Advances in pig welfare* (Woodhead Publishing), 415–444. doi: 10.1016/B978-0-08-101012-9.00014-9

Lawrence, A. B., Vigors, B., and Sandøe, P. (2019). What is so positive about positive animal welfare? -a critical review of the literature. Woodhead Publishing, Sawston, Cambridge, UK *Animals* 9 (10), 783. doi: 10.3390/ani9100783

Leng, G., Leng, R. I., and Ludwig, M. (2022). Oxytocin–a social peptide? deconstructing the evidence. *Philos. Trans. R. Soc. B* 377 (1858), 20210055. doi: 10.1098/rstb.2021.0055

Lindquist, K. A., Satpute, A. B., Wager, T. D., Weber, J., and Barrett, L. F. (2016). The brain basis of positive and negative affect: evidence from a meta-analysis of the human neuroimaging literature. *Cereb. Cortex* 26, 1910–1922. doi: 10.1093/cercor/bhv001

Lovén Wallerius, M., Johnsson, J. I., Cooke, S. J., and Arlinghaus, R. (2020). Hook avoidance induced by private and social learning in common carp. *Trans. Am. Fisheries Soc.* 149, 498–511. doi: 10.1002/tafs.10246

McLennan, K., and Mahmoud, M. (2019a). Development of an automated pain facial expression detection system for sheep (*Ovis aries*). *Animals* 9 (4), 196. doi: 10.3390/ani9040196

McLennan, K. M., Miller, A. L., Dalla Costa, E., Stucke, D., Corke, M. J., Broom, D. M., et al. (2019b). Conceptual and methodological issues relating to pain assessment in animals: the development and utilisation of pain facial expression scales. *Appl. Anim. Behav. Sci.* 217, 1–15. doi: 10.1016/j.applanim.2019.06.001

Mellor, D. J. (2015). Enhancing animal welfare by creating opportunities for positive affective engagement. *N. Z. Vet. J.* 63, 3–8. doi: 10.1080/00480169.2014.926799

Mendl, M., Held, S., and Byrne, R. W. (2010). Pig cognition. *Curr. Biol.* 20, R796–R798. doi: 10.1016/j.cub.2010.07.018

Mendl, M., and Paul, E. S. (2004). Consciousness, emotion and animal welfare: insights from cognitive science. *Anim. Welfare* 13, 17–25. doi: 10.1017/S0962728600014330

Mendl, M., and Paul, E. S. (2020). Animal affect and decision-making. *Neurosci. Biobehav. Rev.* 112, 144–163. doi: 10.1016/j.neubiorev.2020.01.025

Meyer-Lindenberg, A., Domes, G., Kirsch, P., and Heinrichs, M. (2011). Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine. *Nat. Rev. Neurosci.* 12, 524–538. doi: 10.1038/nrn3044

Muri, K., Stubsjøen, S. M., Vasdal, G., Moe, R. O., and Granquist, E. G. (2019). Associations between qualitative behaviour assessments and measures of leg health, fear and mortality in Norwegian broiler chicken flocks. *Appl. Anim. Behav. Sci.* 211, 47–53. doi: 10.1016/j.applanim.2018.12.010

Nicol, C. J., Caplen, G., Edgar, J., and Browne, W. J. (2009). Associations between welfare indicators and environmental choice in laying hens. *Anim. Behav.* 78, 413–424. doi: 10.1016/j.anbehav.2009.05.016

Parker, K. J., Buckmaster, C. L., and Lyons, D. M. (2005). Intranasal oxytocin administration attenuates the ACTH stress response in monkeys. *Psychoneuroendocrinology* 9, 924–929. doi: 10.1016/j.psyneuen.2005.04.002

Perez, O. D., and Dickinson, A. (2020). A theory of actions and habits: the interaction of rate correlation and contiguity systems in free-operant behavior. *Psychol. Rev.* 127, 945. doi: 10.1037/rev0000201

Phillips, M. L., Bullmore, E. T., Howard, R., Woodruff, P. W., Wright, I. C., Williams, S. C. R., et al. (1998). Investigation of facial recognition memory and happy and sad facial expression perception: an fMRI study. *Psychiat. Res. Neuroimag.* 83, 127–138. doi: 10.1016/S0925-4927(98)00036-5

Poirier, C., Bateson, M., Gualtieri, F., Armstrong, E. A., Laws, G. C., Boswell, T., et al. (2019). Validation of hippocampal biomarkers of cumulative affective experience. *Neurosci. Biobehav. Rev.* 101, 113–121. doi: 10.1016/j.neubiorev.2019.03.024

Pruitt, J. N., Burghardt, G. M., and Riechert, S. E. (2012). Non-conceptive sexual behavior in spiders: a form of play associated with body condition, personality type, and male intrasexual selection. *Ethology* 118, 33–40. doi: 10.1111/j.1439-0310.2011.01980.x

Rayner, A. C., Newberry, R. C., Vas, J., and Mullan, S. (2020). Slow-growing broilers are healthier and express more behavioural indicators of positive welfare. *Sci. Rep.* 10, 1–14. doi: 10.1038/s41598-020-72198-x

Rolls, E. T. (2005). *Emotion explained* (Oxford, UK: Oxford University Press).

Ross, H. E., and Young, L. J. (2009). Oxytocin and the neural mechanisms regulating social cognition and affiliative behavior. *Front. Neuroendocrin* 30, 534–547. doi: 10.1016/j.yfrne.2009.05.004

Rousing, T., Bonde, M., and Sørensen, J. T. (2001). Aggregating welfare indicators into an operational welfare assessment system: a bottom-up approach. *Acta Agric. Scand. Sect. A Anim. Sci.* 51, 53–57. doi: 10.1080/090647001300004790

Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., et al. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orang-utans in a complex foraging task derived from cleaner – client reef fish cooperation. *PloS One* 7, e49068. doi: 10.1371/journal.pone.0049068

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

Smith, A. S., and Wang, Z. (2012). Salubrious effects of oxytocin on social stress-induced deficits. *Horm. Behav.* 61, 320–330. doi: 10.1016/j.yhbeh.2011.11.010

Sorge, R. E., Martin, L. J., Isbester, K. A., Sotocinal, S. G., Rosen, S., Tuttle, A. H., et al. (2014). Olfactory exposure to males, including men, causes stress and related analgesia in rodents. *Nature. Methods* 11, 629–634. doi: 10.1038/nmeth.2935

Spruijt, B. M., van den Bos, R., and Pijlman, F. T. (2001). A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Appl. Anim. Behav. Sci.* 72, 145–171. doi: 10.1016/S0168-1591(00)00204-5

Tarazona, A. M., Ceballos, M. C., and Broom, D. M. (2020). Human relationships with domestic and other animals: one health, one welfare, one biology. *Animals* 10, 43. doi: 10.3390/ani10010043

Thorstad, E. B., Næsje, T. F., Fiske, P., and Finstad, B. (2003). Effects of hook and release on Atlantic salmon in the river alta, northern Norway. *Fisheries Res.* 60, 293–307. doi: 10.1016/S0165-7836(02)00176-5

Toates, F. (2002). "Physiology, motivation and the organization of behaviour," in *Ethology of domestic animals – an introduction*. Ed. P. Jensen (Wallingford, UK: CABI).

Tost, H., Champagne, F. A., and Meyer-Lindenberg, A. (2015). Environmental influence in the brain, human welfare and mental health. *Nat. Neurosci.* 18, 4120–4131. doi: 10.1038/nn.4108

van der Harst, J. E., Fermont, P. C. J., Bilstra, A. E., and Spruijt, B. M. (2003). Access to enriched housing is rewarding to rats as reflected by their anticipatory behaviour. *Anim. Behav.* 66, 493–504. doi: 10.1006/anbe.2003.2201

Webb, L. E., Veenhoven, R., Harfeld, J. L., and Jensen, M. B. (2019). What is animal happiness? *Annls N. Y. Acad. Sci.* 1438, 62–76. doi: 10.1111/nyas.13983

Wemelsfelder, F. (2007). How animals communicate quality of life: the qualitative assessment of animal behaviour. *Anim. Welfare* 16, 25–31. doi: 10.1017/S0962728600031699

Würbel, H. (2009). Ethology applied to animal ethics. *Appl. Anim. Behav. Sci.* 118, 118–127. doi: 10.1016/j.applanim.2009.02.019

Yeates, J. W., and Main, D. C. (2008). Assessment of positive welfare: a review. *Vet. J.* 175, 293–300. doi: 10.1016/j.tvjl.2007.05.009

Zentall, T. R. (2021). Effect of environmental enrichment on the brain and on learning and cognition by animals. *Animals* 11 (4), 973. doi: 10.3390/ani11040973