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Webb, Laura E.; Veenhoven, Ruut; Harfeld, Jes Lynning; Jensen, Margit Bak

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## ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

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REVIEW

## What is animal happiness?

Laura E. Webb,<sup>1</sup> Ruut Veenhoven,<sup>2,3</sup> Jes Lynning Harfeld,<sup>4</sup> and Margit Bak Jensen<sup>5</sup>

<sup>1</sup>Animal Production Systems Group, Department of Animal Science, Wageningen University & Research, Wageningen, the Netherlands. <sup>2</sup>Erasmus University Rotterdam, Erasmus Happiness Economics Research Organization (EHERO), Rotterdam, the Netherlands. <sup>3</sup>Optentia Research Program, North-West University, Vanderbijlpark, South Africa. <sup>4</sup>Department of Learning and Philosophy, Centre for Applied Philosophy, Aalborg University, Aalborg, Denmark. <sup>5</sup>Department of Animal Science – Behaviour and Stress Biology Group, Aarhus University, Tjele, Denmark

Address for correspondence: Laura E. Webb, Animal Production Systems Group, Department of Animal Science, Wageningen University & Research, POB 338, 6700 AH Wageningen, the Netherlands. [laura.webb@wur.nl](mailto:laura.webb@wur.nl)

Today, we see a growing concern for the quality of life of nonhuman animals and an accompanying call for viable means of assessing how well animals thrive. Past research focused on minimizing negatives such as stress, while more recent endeavors strive to promote positives such as happiness. But what is animal happiness? Although often mentioned, the term lacks a clear definition. With recent advances in the study of animal emotion, current interest into positive rather than negative experiences, and the call for captive and domesticated animals to have good lives, the time is ripe to examine the concept of animal happiness. We draw from the human and animal literature to delineate a concept of animal happiness and propose how to assess it. We argue that animal happiness depends on how an individual feels generally—that is, a typical level of affect.

**Keywords:** animal welfare; human happiness; typical level of affect; affect balance

### Introduction

There is increasing public concern for the treatment of captive and domesticated animals, including laboratory, farm, work, zoo, companion, and managed wild animals. Western societies now call for “a good life” for these animals.<sup>1–3</sup> A concern for animal welfare is based on the acceptance of animal sentience, which is defined as the capacity to feel pain and pleasure. The traditional approach to animal welfare was that pain, suffering, distress, and other negative physical or mental experiences should be minimized.<sup>4</sup> Consequently, there is a bias in the science of animal welfare toward the study of negative experiences at the expense of positive ones.<sup>5</sup> Advances in our understanding of animals, in particular mammals, and the associated evolution in societal views have led to the gradual inclusion of positive experiences into definitions and assessments of animal welfare.<sup>4,6,7</sup> It is now evident that although the study of negative experiences may have more moral urgency, simply aiming at an absence of negative experiences cannot translate into a good life.<sup>3,6</sup>

The increased focus on the positive has been paralleled by an increased interest in the emotional lives, or affective states, of animals, from a conceptual and practical point of view.<sup>8–10</sup> As with definitions of animal welfare, definitions of affect, whether in relation to animals or humans, are diverse. It is generally agreed that affect is a subjective experience that varies in pleasantness or unpleasantness (valence) as well as activation (arousal).<sup>11</sup> In line with an increased interest in animal affect, a growing body of methodologies to assess affect in animals are being proposed.<sup>12</sup> These methodologies involve the measurement of physiological, behavioral, or cognitive variables thought to vary with, or be an inherent part of, affective experiences.<sup>9</sup>

### Questions

With a growing interest in promoting positive experiences and the call for a good life, the concept of animal happiness requires exploration. Although a number of articles addressing animal welfare mention the term *animal happiness*, this term is either not defined<sup>3,13–17</sup> or defined inconsistently, with authors sometimes referring to a personality trait,<sup>6</sup>

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### Box 1: Happiness and philosophy

Throughout the ages, philosophers have contemplated the definition of a good life. Aristotle (384–322 BC) developed a theory of happiness (eudaimonia) that focused on fulfilling an ideal human life and living life according to the virtues.<sup>20</sup> Epicurus (341–270 BC) reasoned that happiness was to be in a state of *ataraxia*, which means to be untroubled by worries or to be content.<sup>21</sup> Most premodern thinkers do not attribute the concept of happiness to animals. This was not necessarily because they did not attribute positive affective experiences to animals but because they were concerned with the concept of happiness as a phenomenon connected to higher cognitive abilities such as abstract reasoning, seeing the meaning in one's life and assessing one's situation across past and future; abilities that we do not readily attribute to animals. By the 18th century, such diverse thinkers as Jean-Jacques Rousseau and Jeremy Bentham had started including animals into their normative theories due to animals' presumed ability to experience pain and pleasure.<sup>22,23</sup>

a short-term emotion or a longer term mood,<sup>6,8,12</sup> or providing a vague definition.<sup>6</sup> Yet others equate happiness with quality of life and apply a definition similar to that found in the human literature.<sup>18</sup> Given the inconsistent use of the term *happiness* in the context of animal welfare, the time is ripe to consider the concept of animal happiness and answer the following key questions: What exactly is animal happiness? How does animal happiness relate to animal welfare? and How can we assess animal happiness?

#### Approach

The study of human welfare, or quality of life, has benefited from many more years of thought and study, and from the human capacity to report subjective feelings verbally. Human psychology research provides animal researchers with new insights into potential definitions and methods.<sup>19</sup> The aim of our review is to propose a framework for the concept and assessment of animal happiness. To this end, we first study the literature on human quality of life, in particular, human happiness, and identify concepts that may also apply to animals and compare these with notions of animal welfare. Following this, possible methodologies to assess the proposed concept of animal happiness are examined.

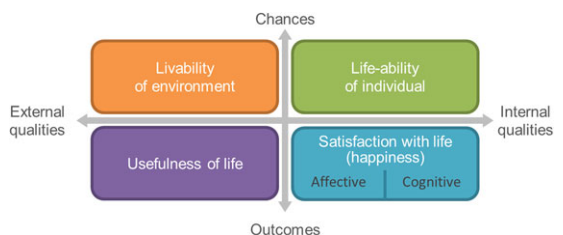
#### Human happiness

The concept of human happiness has been examined for millennia by philosophers (Box 1), and for just over a century by psychologists. In humans, happiness has been related to quality of life, including satisfaction with life and well-being, and the meanings of these terms must hence be briefly presented before we examine the concept of human happiness.

#### Four different notions of human quality of life

There are many notions, or views, of human quality of life and these can be sorted into a fourfold matrix<sup>24</sup> (Fig. 1): (1) livability of the environment, (2) life-ability of the individual, (3) usefulness of life, and (4) satisfaction with life. This matrix draws on two distinctions. The first distinction is between the *chances* for a good life and the actual *outcomes* of a life, with chances and outcomes being related but not the same; individuals may fail to realize chances, but they may also make much out of poor chances. The second difference is between external (in the environment) and internal (in the individual) qualities. External and internal qualities refer to conditions of which an individual need not be aware of subjectively to have a high quality of life.

Liveability of the environment represents the view that human quality of life has to do with the quality of living conditions. This view refers explicitly to a characteristic of the environment and does not have the limited connotation of material conditions.



**Figure 1.** The four different views of human quality of life, based on Veenhoven.<sup>24</sup> The matrix draws a distinction between chances for a good life and the outcomes of a life, and between external (environmental) and internal (individual) qualities. A distinction is also made between cognitive and affective appraisals linked to the satisfaction with life quadrant.

One could also speak of the “habitability” of an environment. Contemporary economists often refer to this as “welfare” or “standard of living.”<sup>25,26</sup>

Life-ability of the individual represents the view that human quality of life has to do with how well individuals are equipped to cope with challenges. Doctors and psychologists use the terms *quality of life* and *well-being* to denote this specific meaning.<sup>27</sup> In biology, the phenomenon is referred to as adaptive potential<sup>28</sup> and in health care as health.<sup>29</sup> Psychological terms include *efficacy* and *potency*.<sup>30</sup> Life-ability will typically add to a subjective appreciation of life (bottom-right quadrant), but should not be equated with that. Even the best life-abilities can fail to overcome severe environmental challenges, and the benefits of specific life-abilities depend on which environment one lives in.

Usefulness of life represents the view that human quality of life has to do with higher values. In other words, a good life is one that is good for something other than itself, it should have a meaning and purpose, such as a commitment to socially shared values. It is sometimes referred to as “the meaning of life,” which then is intended to denote true (objective) significance, instead of a mere subjective sense of meaning.<sup>31</sup> Note that this external benefit does not require inner awareness. A human’s life may be useful without them knowing, especially if the effects manifest after their death. A useful life is not necessarily a happy life, for instance, not when one sacrifices one’s personal happiness for a greater good.<sup>32</sup> Only aspects of usefulness for which an individual is aware may impact on the subjective appreciation of life (bottom-right quadrant).

Satisfaction with life represents the view that human quality of life is in the eye of the beholder and designates “subjective appreciation of one’s life as a whole.” This is commonly referred to using terms such as subjective well-being,<sup>33</sup> life satisfaction,<sup>34</sup> and happiness<sup>35</sup> in a limited sense of this word. Much of the present day happiness research focuses on this human quality of life, and human happiness can hence be defined as the enjoyment of one’s life as a whole. A life will have more of this quality, the more and the longer a life is enjoyed. The four views of the human quality of life described above are causally interrelated. Chances for a good life affect outcomes of life, but inversely outcomes can also affect changes; satisfaction with life (outcome) can foster life-abilities such as resilience (chances).

### *Assumed and apparent quality of life*

The term *quality of life* includes four separate notions. The first three of these notions are the assumed quality of life, while the last one, happiness (also referred to as satisfaction with life), is the apparent quality of life. Most research on human quality of life aims at identifying optimal life-chances, that is, environmental conditions that policies should provide, and inner capabilities that education should cultivate (upper two quadrants in Fig. 1). Yet, it is easier to count the presence of such conditions than to ascertain that they are really required for a good life, and if relevant, to what degree, in what combinations, and for what kinds of people. Hence, notions of livability and life-ability depend heavily on values and, for that reason, common sum-scores of life-chances reflect assumed quality of life.<sup>36</sup> Whether such combinations actually result in a good life is determined by how long and happy people live, which Veenhoven calls apparent quality of life.<sup>36</sup> In his view, we can identify good life-chances (top two quadrants in Fig. 1) by studying happiness levels in different cases (right bottom quadrant).

### *Two components of human happiness*

Happiness was defined above as the enjoyment of one’s life as a whole. When appraising how happy they are, humans draw upon two sources of information: (1) how well their life-as-it-is compares to standards of how they believe life should be (conscious demands) and (2) how well they feel in general. These subappraisals are seen as components of happiness; the cognitive component and the affective component, respectively.<sup>37–40</sup> Although the cognitive and affective components of happiness represent different mechanisms, they are found to strongly correlate.<sup>34</sup>

**Cognitive component.** Bentham<sup>22</sup> thought of happiness as the end product of a mental calculus. Many scholars in the field also see it as the result of a cognitive process—a weighted average of earlier life-aspect evaluations<sup>41</sup> or a series of comparisons of life-as-it-is with various standards of how-life-should-be.<sup>42</sup> The cognitive component of happiness requires conscious awareness: Do I get what I want from life? Veenhoven refers to the cognitive component of happiness as “contentment,” in essence, the “degree to which an individual perceives that his or her aspirations are met.”<sup>43</sup>

Note that this component of happiness has no connection to the cognitive component of affect, which has to do with the bidirectional link between affect, on the one hand, and judgment, attention, and memory, on the other hand.<sup>44</sup>

**Affective component.** Individuals who experience positive affect frequently and negative affect infrequently report high levels of happiness.<sup>40</sup> This affective component of happiness includes both positive and negative affect, which are thought to be regulated by separate dedicated systems.<sup>32,45,46</sup> Positive affect is thought to be regulated by the behavioral activation system, which promotes approach, while negative affect is thought to be regulated by the behavioral inhibition system, which promotes avoidance.<sup>45</sup> Evolutionary biologists propose that individuals receive a positive affective signal for events that help them thrive and adapt to the environment and a negative affective signal for events that compromise survival or reproductive success.<sup>47</sup> As Spruijt *et al.*<sup>48</sup> state, “Under normal conditions those things that are pleasurable, i.e. causing and reinforcing behavior at this moment, are those things that are good in the long run, i.e. have high fitness value.” This implies that under nonnatural conditions, such as those linked to modern living, pleasurable things may, in fact, lead to low fitness in the long run. This low fitness may, in turn, be linked to a high frequency of negative experiences, for example, those linked to being overweight, tired or ill from eating high-fat and high-sugar foods, which will subsequently lead to low levels of affective happiness.

It is the frequency, not the intensity, of affect that seems to have the highest weight in overall reports of happiness:<sup>40</sup> humans reporting high levels of happiness do not experience more intense positive emotions, but rather more frequent positive emotions of average intensity.<sup>49</sup> Therefore, affective happiness, although sometimes referred to as the average level of affect, is based on the frequency of positive and negative affect (separately or the ratio thereof) and not per se on an average, which would imply that the intensity/value of each transient emotion or mood is of importance. Moreover, the affective component of happiness does not require conscious awareness.<sup>50</sup> One can feel well most of the time without being aware of one’s typical level of affect. In essence, affective happiness is a background typical



**Figure 2.** Schematic representation of the distinction between emotion, mood, and affective happiness. Although emotions and moods are transient affective experiences, affective happiness is stable under more or less stable conditions.

level of affect that one may only become aware of when one needs to report it.

Affective happiness cannot be equated with emotions and moods. Moods are generally defined as affective states that are derived from the cumulative experience of shorter term (acute) emotions, which occur in response to specific external or internal stimuli.<sup>8</sup> Moods are transient states and are generally said to last hours to weeks.<sup>51</sup> Affective happiness, that is, hedonic or typical level of affect, draws on affective experiences, such as emotions and moods, but is not the same. Affective happiness is not an emotion or a mood but the frequency of pleasantness in all affective experiences. All affective states are transitory, but the frequency of positive and negative affect, that is affective happiness, can be quite stable (Fig. 2). Since affective happiness is defined as how well one feels most of the time, it has some stability by definition. This is not to say that affective happiness is a fixed trait; how well one feels on the balance is basically a state though typically reproduced in stable conditions. In livable conditions, we tend to feel well, that is, experience more positive than negative affect, studies in contemporary affluent societies showing ratios of around 3 to 1.<sup>52</sup>

There are good reasons to believe that overall happiness is mainly extrapolated from affective rather than cognitive experience.<sup>34</sup> One reason for this is that “life-as-a-whole is not a suitable object for calculative evaluation.”<sup>53</sup> Life has many facets and there is generally no straightforward ideal to compare it with. Another reason seems to be that cognitive appraisals are often instigated by affective cues.<sup>54</sup> This corresponds with the theory that affective systems are evolutionarily older than cognition and that cognition works as an addition to the navigation system rather than as a replacement.<sup>55</sup>

## Notions of animal welfare and links to human quality of life and happiness

### *Notions of animal welfare*

In modern animal welfare research, three main views of animal welfare have been identified by Fraser: (1) basic health and functioning, (2) natural living, and (3) affective states.<sup>13,14</sup>

The basic health and functioning view places emphasis on freedom from disease, injury, and stress, and meeting basic requirements for life, including appropriate nutrition, water, and so on. Criticism of this view by adherents of other views includes the concern that a perfectly healthy and well-functioning animal may still be housed in an environment providing little stimulation, hence little opportunity for positive experiences, possibly leading to negative affective states of boredom, frustration, or depression.<sup>13</sup>

The natural living view places emphasis on the level of “naturalness” in the lives of animals—on the importance of natural species-specific behaviors and on an environment containing natural elements.<sup>13</sup> Some would argue that the welfare of animals is improved the closer they are maintained to their natural, wild state.<sup>56</sup> Adherents of other views criticized the natural living view based on the fact that wild ancestors of domesticated species may have faced difficult challenges, such as poor nutritional or climatic conditions. There is also the difficulty of deciding what exactly constitutes natural behaviors or environments for highly selected, domesticated animals.

The affective states view places emphasis on the feelings of animals.<sup>14</sup> This view focuses on minimizing negative affect and maximizing positive affect. This view is based on the assumption that animals can subjectively experience their feelings, necessitating some basic form of consciousness, which is often referred to as a sentience—the ability to experience pain and pleasure.<sup>3,57,58</sup>

These three views of animal welfare, as with the four notions of human quality of life, interrelate and show some overlap.<sup>13</sup> Many animal welfare authors suggest that all three of these notions should be combined to obtain the most accurate and complete definition of animal welfare.<sup>13,59</sup> If these three views are combined into a unified definition of animal welfare, it follows logically that they must be considered as equally important components of animal wel-

fare. Many researchers and stakeholders, however, will favor one of these views. Below, we compare these three views to the notions of human quality of life and to the different components of human happiness.

### *How do the notions of animal welfare compare to those of human quality of life?*

The basic health and functioning view of animal welfare can be related to internal chances, that is, how well individuals are equipped to cope with challenges (e.g., immunity and resilience). Natural living in animals has to do with the livability of the environment and the extent to which this is linked to the adaptive repertoire of individuals (life-ability). Natural living can thus be related to both external and internal qualities of the chances axes in the human quality of life framework (Fig. 1). The affective states view of animal welfare is an internal outcome, and can hence be linked to human satisfaction with life or happiness. The affective states view of animal welfare might hence be equated with, or part of, animal happiness. To determine whether the affective states view is animal happiness or only part of this concept, we must first compare the three views of animal welfare to the components of human happiness.

The human quality of life *usefulness* is not represented in our selected animal welfare concepts. However, given that animal welfare becomes a point of concern in animals used for human benefit, and hence with some usefulness, it seems that usefulness is an inherent part of all animal welfare discussions.

### *How do the components of animal welfare compare to components of human happiness?*

We will now consider the three views of animal welfare described above, as integrated components of a unified animal welfare concept and compare them to the components of human happiness, namely the satisfaction with life view of the human quality of life. As mentioned above, human happiness draws from two separate components: affective and cognitive. In human happiness research, health or (natural) living conditions are not included as components of happiness, but rather as factors that impact on human happiness<sup>60</sup> or possible outcomes/consequences of happiness.<sup>61,62</sup> Only affect

is included as a component of both animal welfare and human happiness.

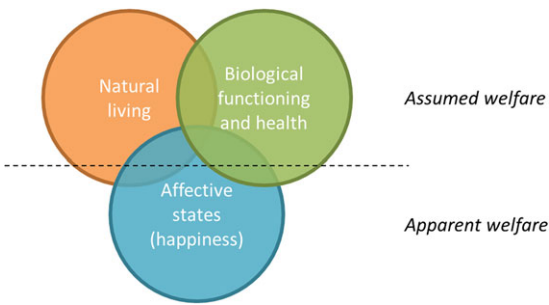
Vertebrate animals are sometimes accepted as sentient beings based on evidence that they can feel both pain and pleasure (see Ref. 5). If animals can feel good or bad, the concept of a typical level of affect, or the affective component of human happiness, applies; even if animals are not aware of their frequency.<sup>50</sup> In this respect, animals might be comparable to human infants.<sup>63</sup> The importance of affect to animal welfare, and in particular the importance of the balance between positive and negative affective experiences, is reflected in previously proposed definitions of animal welfare (see Ref. 64 for a review of frameworks of positive animal welfare). Simonsen<sup>65</sup> defined animal welfare as “the animal’s positive and negative experiences.” McMillan<sup>66</sup> proposed that animal quality of life, which is now roughly accepted as synonymous with animal welfare,<sup>17</sup> “may be viewed as a set of scales, with pleasant feelings on one side and unpleasant feelings on the other.”<sup>67</sup> Yeates and Main<sup>68</sup> proposed that animal welfare is based on everyday sensational pleasures, among other things. Finally, Green and Mellor<sup>3</sup> argued that a good animal life could be defined as a life where “the balance of salient positive and negative experiences is strongly positive.” Many other applied ethologists have also emphasized the important role of affect or affect balance in the study of animal welfare or quality of life.<sup>6,8,48,69,70</sup>

With respect to a possible cognitive component of animal happiness, many definitions of animal welfare propose that some level of cognitive activity is involved in the level of welfare an animal experiences. Yeates and Main<sup>68</sup> emphasize the importance of allowing individuals to realize their own goals. Franks and Higgins<sup>19</sup> suggest that animal welfare is a function of needs satisfaction and that it is based on the ability to realize own goals, gather information, and have some level of control over the environment. Finally, McMillan<sup>67</sup> writes, “Quality of life is the affective and cognitive (to the degree that the animal can form such a cognitive construct) assessment that an animal makes of its life overall,” which very closely resembles current definitions of human happiness. Animals have goals that they are motivated to reach, in that they are willing to work hard to achieve them; when increasing cost is placed on fulfilling these goals, animals will increase their rate of work to achieve them.<sup>71</sup> This is not only the

case for physiological necessities such as food. Animals will go a long way to defend access to aspects, such as social contact, novelty, and occupation.<sup>72–74</sup> Animals, moreover, display individual preferences that are linked to liking (see Ref. 75). Animals show indications of increased welfare when their goals are met and preferences catered for. For instance, play behavior is observed in juveniles of many species in the absence of welfare threats.<sup>76</sup> But see Ref. 77 for a recent critical review of the link between welfare and play.

It is, however, unclear to what extent animals are able to conceptualize the degree to which their goals are met and it is thus unknown whether the cognitive component seen in human happiness is also present in (certain) species of animals. We take the tentative stance that the happiness level of (most) vertebrate animals probably depends much more, if not only, on the affective component of happiness. This is supported by the fact that even in the most cognitively complex species on Earth, that is humans, the cognitive component takes a secondary position relative to the affective component.<sup>34</sup> Further research will have to determine whether certain animals can conceptualize to which degree their life meets their standards.

Given the above reflection on how different concepts of animal welfare can be related to the human qualities of life views and human happiness components, we define animal welfare comparably to Fraser,<sup>13</sup> but also similarly to human quality of life, in terms of various views that are interrelated but separate. The affective states view corresponds to an internal outcome and can hence be linked to animal happiness as far as it can be conceptualized in a manner similar to that in humans. As with humans, we can speculate about the environmental conditions and the individual capabilities that make for a good life for particular kinds of animals and individuals within that species, and the apparent importance of these will depend greatly on the individual animal, on people’s values, and on our current understanding of the species at that given moment. On that basis, environmental conditions and individual capabilities estimate assumed quality of life. For example, we can ask animals to indicate preferences for various resources, but these preferences will depend on the options presented, which are themselves dependent on human choices. Moreover, we may assume that sick animals have low



**Figure 3.** Linking the views of animal welfare as identified by Fraser *et al.*<sup>14</sup> with the concept of animal happiness, defined in terms of affect balance. Natural living and biological functioning are linked to assumed welfare, because various environmental or psychological aspects are assumed to be better for welfare (e.g., more natural environment or good health). Affective states instead are linked to apparent welfare, because it is based on assessing the subjective experience of an animal. When affective states are investigated in the context of an individual's life as a whole, this view of animal welfare can be translated as animal happiness.

levels of happiness, but this may not be the case if the disease does not impact on the subjective experiences of the animals. The only way to establish how a particular resource or disease impacts animal happiness is to study apparent quality of life and hence attempt to assess how happy animals feel (affective states view), and on that basis, infer in what conditions they do best, rather than assume what is good for them (Fig. 3).

### Measures of affective happiness in humans

Above, we defined affective happiness as “how well one feels most of the time.” In humans, this can be measured in several ways. The most common way is to use self-reports of how well one feels generally (trait approach) or repeated self-reports of how well one feels now (summed state approach). How one feels generally, hence the trait approach to affective happiness, is not the same as measuring mood, as stated above. Self-reports are the gold standard in human happiness research. Not all humans, however, are able to report how they feel, for example, human infants; for these cases, several nonverbal measures have been developed, which focus either on typical affect level or on affect at one given moment with the ultimate aim of computing the ratio of pleasant and unpleasant affect, that is, affect balance. Nonverbal indications of affect are

seen in expressive behaviors and in physiological attendants of pleasant and unpleasant experiences. These different approaches are introduced below with some examples. There has been much more research into markers of cumulative negative experiences but the focus here is on measures that can go into the positive as well as negative ranges of affective happiness. We will hence not describe in detail measures of chronic stress or depression.

### Trait approaches—estimates of typical affect

Typical affect can be assessed nonverbally using proxy reports, which are estimates made by humans who know an individual of interest well, such as a parent or a friend. Such ratings draw upon both verbal and nonverbal communications from the individual of interest. Studies that compare sick children or adolescent self-reports of happiness to parent proxy reports find a gap between the two, indicating that proxy reports, at least those of parents, are not always accurate reports of happiness.<sup>78,79</sup> Behavioral measures include systematic observations of nonverbal behaviors deemed indicative of a human's typical level of affect and are commonly made by teachers and therapists, usually using an observation schedule such as the German “Allensbacher Ausdrücktest,” which involves facial expression and body posture. A study that compared interviewer rating on the Allensbacher with respondent's self-reports found modest correlations of around +0.40.<sup>80</sup>

Typical affect has been shown to influence human physiology on three levels: the neuroendocrine, immune, and cardiovascular<sup>81–84</sup> level, thus physiological response may be a valid nonverbal indicator of the typical level of affect. For example, repeated positive affect has been linked to lower plasma fibrinogen during a single stress test.<sup>82</sup> Fibrinogen is a positive acute phase protein, the plasma levels of which rise in response to inflammation. Single physiological markers, however, vary in response to many different factors, including disease, which makes them not entirely reliable when it comes to assessing affective happiness. A better marker could be a composite indicator. One example of a composite indicator of cumulative biological risk reflecting complex multisystemic dysregulation is the allostatic load (AL) model.<sup>85–87</sup> AL increases with accumulated stress and can be measured at a single time point by recording the levels of a number of



biomarkers.<sup>87</sup> Exact biomarkers used and formulations and statistical tests applied vary per study and there is hence not one accepted method to assess AL.<sup>87</sup> Next to an accumulation of stress, AL was recently also linked to an accumulation of positive affect, and could hence be used as a physiological indicator of typical affect.<sup>88</sup>

Another method to assess typical affect is to investigate brain structure and function. There is no single pleasure center in the brain; instead, hedonic valence seems to be generated by a set of limbic and paralimbic brain structures.<sup>89,90</sup> Major depressive disorder, for example, is linked to changes in the size of certain brain structures<sup>91</sup> and Urry *et al.*<sup>92</sup> found greater left than right superior frontal activation associated with higher levels of both affective and cognitive components of happiness. Prefrontal activation asymmetries linked to emotions and affective happiness are reviewed by Davidson<sup>93</sup> and Davidson *et al.*<sup>94</sup> Affective happiness was, moreover, linked to fractional amplitude of low-frequency fluctuations in the right amygdala.<sup>95</sup> For a review on brain changes linked to chronic stress, see Ref. 96.

At the genetic level, there is evidence that individuals with the transcriptionally more efficient version of the serotonin transporter gene report significantly higher levels of typical affect.<sup>97</sup> Typical affect is also linked to telomere length, with shorter telomere length being associated with repeated stress,<sup>98</sup> and vice versa.<sup>99</sup> Finally, gut microbiota was linked to depression and positive mood,<sup>100</sup> and may hence in the future prove useful in assessing affective happiness in humans.

### *Summed states approach—estimates of affect balance*

Another way to assess typical hedonic level is to use multiple-moment observations to compute affect balance: the ratio of pleasant to unpleasant affect. First, one can repeatedly request self-reports of momentary affect from individuals. This technique is referred to as the experience sampling method (ESM) and typically involves sending signals to individuals via their smartphones at random times of the day, on average seven times per day for 1 week, to ask how they are feeling in that precise moment.<sup>101</sup> The day reconstruction method is a variant of ESM in which respondents first list their activities of the previous day and then rate how well they have felt during each of these activities.<sup>102</sup> Second, one can

sample expressive behaviors, such as laughing or weeping, at regular time intervals; the method is referred to as time sampling. This method has been used to measure affect balance in human infants using the frequency of smiling and laughing versus crying.<sup>63</sup> Finally, some physiological measure can be repeatedly sampled in humans to compute affect balance, for example, salivary cortisol<sup>82,103</sup> or heart rate (in men),<sup>82</sup> with a higher frequency of positive affect across the day being linked to lower average cortisol and heart rate over the day.

### **Measures of affective happiness in animals**

The study of animal affect has grown over the past decades and we now know of several possible, more or less validated methodologies that can be used to assess animal affect.<sup>6,12,104,105</sup> With animals, we lack the gold standard of self-reports and must make use of indirect indicators of affect instead. These include behavioral indicators of momentary affect (e.g., spontaneous postures and behaviors, facial expressions, vocalizations, approach or avoidance responses to novel stimuli), cognitive biases linked to particular affective states (judgment, attention, and memory), or physiological changes linked to acute or chronic affect (e.g., oxytocin).<sup>106–110</sup> Physiological indicators of both momentary and long-term affect include neuroendocrine,<sup>106</sup> immune,<sup>6</sup> and cardiovascular changes,<sup>111</sup> as in humans. We do not describe these behavioral, cognitive, or physiological methods in detail here as these are reviewed elsewhere.<sup>6,9,12,104,105</sup> We do, however, point to how these methods can be applied to our concept of animal happiness. Moreover, as in humans, there has been much research into markers of chronic stress<sup>112–114</sup> and depression<sup>115,116</sup> in animals, usually in laboratory animals used to study human pathologies, but we once again will focus on measures that have been found to tap into the positive range of affective happiness.

### **Trait approach—estimates of typical affect**

The judgment bias test (JBT) is used to assess changes in judgment of ambiguity (optimism) in animals.<sup>108</sup> The theory is that cumulative experience of positive and negative affect leads to a more or less optimistic judgment of ambiguous cues.<sup>8</sup> If the judgment of ambiguity is based on transient mood as some suggest,<sup>117,118</sup> then JBT does not measure the typical level of affect and is not

a valid method for assessing affective happiness, unless it can be repeated in time, which has been questioned.<sup>119</sup> However, if JBT is measuring a stable, constant affective state instead, which is suggested by studies linking it to depression,<sup>120</sup> then it would be a valid measure of typical affect. To decide which of these scenarios is valid, one will have to compare the results of the JBT with another method that measures affect balance (see below). JBT is associated with some practical and theoretical limitations, as it is time-consuming, often requires testing animals outside of their home environment, and possibly acts as cognitive enrichment, thereby impacting affect in itself.<sup>121–123</sup> These limitations require future research attention. Animal measures of depression, such as sensitivity to reward loss, can be used to assess the typical level of affect, although it is unclear how far into the positive range these measures might tap.<sup>124–127</sup>

Proxy reports of happiness have also been adapted to certain animal species, including great apes and felids.<sup>128–131</sup> For example, the happiness level of chimpanzees, including a component reflecting affect, was rated by familiar keepers and was moderately associated with objective observations of behavior.<sup>128</sup> Similarly, in a method called qualitative behavior assessment, a subjective assessment is used to assess the welfare state of captive and domesticated animals by rating them using terms such as *positively occupied*.<sup>132</sup> Results of this approach have been reported to show variable inter- and intrarater reliability.<sup>133–135</sup> These types of proxy tools may be criticized as being subjective and unreliable. Furthermore, it is unclear whether these methods assess transient emotions or moods, or affective happiness.

Physiological correlates of affective happiness that can be assessed at one moment in time in humans might be applicable to animals, in particular, mammalian species—which share many brain structures and physiological systems with humans. Physiological markers of depression<sup>115</sup> and chronic stress<sup>112</sup> in animals could provide some measure of cumulative stress, however, as in humans, single markers are unlikely to be reliable measures of affective happiness or even affect for that matter. Reviews of physiological correlates of affect in animals have previously been published.<sup>6,12</sup> Markers of cumulative stress, moreover, may fail to capture the positive experiences and hence the positive range of affective

happiness. The concept of AL seems promising for assessing happiness in animals (personal communication by Louise Kremer, Wageningen University & Research, the Netherlands), and has been previously applied to defining the concept of animal welfare.<sup>136–138</sup> Telomere length as a measure of affective happiness in animals is very promising as it presents a measure of cumulative stress as well as cumulative positive experiences.<sup>139</sup> Gut microbiota may also offer interesting possibilities to assess typical level of affect in animals if it were to prove useful in human happiness research.

### *Summed states approach—estimates of affect balance*

If current methods to assess momentary affect in animals are valid and repeatable over a period of time to enable a computation of the frequency of positive and negative affect, as, for example, with time sampling in human infants, they could potentially be used to compute affect balance, hence affective happiness, in animals. As mentioned above, methods to assess transient affect are described in detail elsewhere and will not be covered here. One promising behavioral indicators of acute affect in animals is vocalization. Vocalizations in animals have been found to reflect both affect valence (e.g., frequency and arousal) and arousal (e.g., loudness and duration).<sup>140,141</sup> In rats, for example, two categories of ultrasonic vocalizations (USVs) have been linked to affect.<sup>142</sup> Minimally frequency-modulated 22-kHz USVs emitted in putatively aversive situations have been labeled “alarm calls” and are assumed to reflect negative affect.<sup>143</sup> High-frequency-modulated 50-kHz USVs emitted during putatively positive or rewarding situations are assumed to reflect positive affect.<sup>143–145</sup> Another example is the snorting sound produced by horses that was recently linked to positive affective experiences.<sup>146</sup> Many more studies have linked vocalizations to emotions in various species. The advantage of vocalizations is that they can be recorded and analyzed in an automated fashion, which may allow for long-term computations of affect balance.

Other possible indicators of acute affect that could be repeatedly sampled over time include play behavior, thought to reflect positive emotion<sup>6</sup> (although the heterogeneity of play behavior and differences between juveniles and adults

complicate the use of this indicator in this context, see Ref. 77), certain body, ear, and tail postures that can be linked to positive or negative affect,<sup>107,111,124</sup> facial expressions,<sup>147,148</sup> and potentially also physiological markers.<sup>106</sup> Recording these indicators of affect repeatedly over a period of time would be time-consuming, making those indicators that can be sampled automatically, using, for example, sensors attached to an animal's body, very valuable in this context.

To conclude, there has been very little work to date done on assessing affective happiness in animals, which consequently makes our discussion of how to measure animal happiness rather short in comparison with the rest of this article. Instead, we present possible avenues for future research. Work on assessing momentary animal affect is still in its infancy but has shown promising results, pointing to some more or less practical and reliable behavioral, cognitive, and, to a lesser extent, physiological markers of affect. The repeated recording of these over a set period of time presents a promising avenue for assessing the typical level of affect in animals. Such affect balance methods will require some level of validation, which will be heavily dependent on human happiness research which benefits from the gold standard of verbal self-reports. One possibility would be to use physiological markers of affective happiness validated in humans to validate behavioral and cognitive measures in animals though this will require similar brain structures and physiological systems between the animal species of interest and humans. Once validated in some way by physiology, affect balance methods can subsequently be used as standards to identify trait approach methods, such as possibly the JBT.

One advantage of the affect balance measurements is that it enables us to assess absolute positive and negative states rather than simply relative positive and negative states.<sup>77</sup> A negative ratio—a higher frequency of negative over positive affect—reflects an absolute negative state, with the number of the ratio indicating how negative this is. A positive ratio—a higher frequency of positive over negative affect—reflects an absolute positive state.

## Conclusions and implications

The aim of our review was to delineate a concept of animal happiness, drawing from literature on human quality of life and happiness and on defini-

tions of animal welfare, and to propose possible assessment methods. The growing public concern for the present-day welfare of captive and domesticated animals and the increasing importance of positive experiences in these concerns make this review particularly topical.

We suggest that animal happiness is most likely only based on an affective component of happiness, contrary to human happiness, which draws both on affective experience and cognitive comparison. Animal happiness, we suggest, can hence be defined as how an animal feels most of the time. Animal happiness defined in this way is about the balance of positive and negative affect, hence reflects the view of animal welfare commonly referred to as affective states. However, the typical level of affective happiness cannot be equated with emotions and moods, which represent, in most definitions, short-term and highly variable affective states.<sup>8</sup> Happiness is a long-term, typically stable state, which reflects how one feels most of the time, that is, the typical level of affect. Our review suggests that certain notions of human happiness can be transferred to animals, and other notions, such as the cognitive component of human happiness, cannot, at least on the basis of existing knowledge. We may yet find in future research that certain animal species can conceptualize to what extent their goals are met, and hence form a cognitive appraisal of their happiness level.

We provide here an attempt at a conceptual framework for the understanding and study of animal happiness. Since objective measures of happiness in animals have to date not received much research attention, we advocate further research into assessing affect balance using existing markers of acute affect in animals. We encourage further research on affective vocalizations and the physiological correlates of affect in both humans and other animals. These could potentially provide objective and practical (e.g., automated) assessments of animal happiness in the future. Tools to compute affect balance in individual animals with the aim of assessing animal happiness will help us understand what animals require for a good life, in terms of both environmental and internal qualities.

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### Author contribution

All authors wrote the manuscript.

### Competing interests

The authors declare no competing interests.

### References

1. Farm Animal Welfare Council. 2009. *Farm Animal Welfare in Great Britain: Past, Present and Future*. London: Farm Animal Welfare Council.
2. Yeates, J.W. 2011. Is 'a life worth living' a concept worth having? *Anim. Welf.* **20**: 397–406.
3. Green, T.C. & D.J. Mellor. 2011. Extending ideas about animal welfare assessment to include 'quality of life' and related concepts. *N. Z. Vet. J.* **59**: 263–271.
4. Tannenbaum, J. 2002. The paradigm shift toward animal happiness. *Society* **39**: 24.
5. Shriver, A.J. 2014. The asymmetrical contributions of pleasure and pain to animal welfare. *Camb. Q. Healthc. Ethics* **23**: 152–162.
6. Boissy, A., G. Manteuffel, M.B. Jensen, *et al.* 2007. Assessment of positive emotions in animals to improve their welfare. *Physiol. Behav.* **92**: 375–397.
7. Mellor, D.J. 2016. Updating animal welfare thinking: moving beyond the "five freedoms" towards "a life worth living". *Animals* **6**: 21.
8. Mendl, M., O.H.P. Burman & E.S. Paul. 2010. An integrative and functional framework for the study of animal emotion and mood. *Proc. R. Soc. B Biol. Sci.* **277**: 2895–2904.
9. de Vere, A.J. & S.A. Kuczaj. 2016. Where are we in the study of animal emotions? *Wiley Interdiscip. Rev. Cogn. Sci.* **7**: 354–362.
10. De Waal, F. 2011. What is an animal emotion? *Ann. N.Y. Acad. Sci.* **1224**: 191–206.
11. Russell, J.A. 2003. Core affect and the psychological construction of emotion. *Psychol. Rev.* **110**: 145.
12. Paul, E.S., E.J. Harding & M. Mendl. 2005. Measuring emotional processes in animals: the utility of a cognitive approach. *Neurosci. Biobehav. Rev.* **29**: 469–491.
13. Fraser, D. 2008. Understanding animal welfare. *Acta Vet. Scand.* **50**: S1.
14. Fraser, D., D.M. Weary, E.A. Pajor, *et al.* 1997. A scientific conception of animal welfare that reflects ethical concerns. *Anim. Welf.* **6**: 187–205.
15. Webster, A.J. 2001. Farm animal welfare: the five freedoms and the free market. *Vet. J.* **161**: 229–237.
16. Desire, L., A. Boissy & I. Veissier. 2002. Emotions in farm animals: a new approach to animal welfare in applied ethology. *Behav. Process.* **60**: 165–180.
17. Broom, D. 2007. Quality of life means welfare: how is it related to other concepts and assessed? *Anim. Welf.* **16**: 45–53.
18. Yeates, J. & D. Main. 2009. Assessment of companion animal quality of life in veterinary practice and research. *J. Small Anim. Pract.* **50**: 274–281.
19. Franks, B. & E.T. Higgins. 2012. Effectiveness in humans and other animals: a common basis for well-being and welfare. In *Advances in Experimental Social Psychology*, Vol. 46. J.M. Olson & M.P. Zanna, Eds.: 285–346. San Diego: Elsevier Academic Press Inc.
20. Hursthouse, R. 2006. Applying virtue ethics to our treatment of the other animals. In *The Practice of Virtue – Classic and Contemporary Readings in Virtue Ethics*. J. Welchman, Ed.: 136–155. Indianapolis, IN: Hackett Publishing Company, Inc.
21. Annas, J. 1993. *The Morality of Happiness*. New York, NY: Oxford University Press.
22. Bentham, J. 1996. *The Collected Works of Jeremy Bentham: An Introduction to the Principles of Morals and Legislation*. Oxford: Clarendon Press.
23. Rousseau, J.-J. 1984. *A Discourse on Inequality*. London: Penguin Books.
24. Veenhoven, R. 2000. The four qualities of life: ordering concepts and measures of the good life. *J. Happiness Stud.* **1**: 1–39.
25. Deardorff, A.V. 2014. *Terms of Trade: Glossary of International Economics*. Singapore, Thailand: World Scientific Publishing Co. Pte Ltd.
26. Jonsson, J.O. & V. Östberg. 2010. Studying young people's level of living: the Swedish child-LNU. *Child Indic. Res.* **3**: 47–64.
27. Michalos, A.C. 2017. Social indicators research and health-related quality of life research. In *Connecting the Quality of Life Theory to Health, Well-Being and Education* 25–58. Cham: Springer.
28. Eizaguirre, C. & M. Baltazar-Soares. 2014. Evolutionary conservation—evaluating the adaptive potential of species. *Evol. Appl.* **7**: 963–967.
29. World Health Organization. 2006. Constitution of the World Health Organization—basic documents. Supplement. World Health Organization.
30. Bandura, A. 1982. Self-efficacy mechanism in human agency. *Am. Psychol.* **37**: 122.
31. Battista, J. & R. Almond. 1973. The development of meaning in life. *Psychiatry* **36**: 409–427.
32. Baumeister, R.F., K.D. Vohs, J.L. Aaker, *et al.* 2013. Some key differences between a happy life and a meaningful life. *J. Posit. Psychol.* **8**: 505–516.
33. Diener, E. 2013. The remarkable changes in the science of subjective well-being. *Perspect. Psychol. Sci.* **8**: 663–666.
34. Kainulainen, S. & R. Veenhoven. 2018. Life satisfaction is more a matter of feeling well, than having what you want. EHERO working paper. Erasmus University Rotterdam.
35. de Groot, J.H., M.A. Smeets, M.J. Rowson, *et al.* 2015. A sniff of happiness. *Psychol. Sci.* **26**: 684–700.
36. Veenhoven, R. 2005. Apparent quality-of-life in nations: how long and happy people live. In *Quality-of-Life Research*

- in Chinese, Western and Global Contexts*. D.T.L. Shek, Y.K. Chan & P.S.N. Lee, Eds.: 61–86. Dordrecht: Springer.
37. Diener, E. 2000. Subjective well-being: the science of happiness and a proposal for a national index. *Am. Psychol.* **55**: 34–43.
  38. Diener, E., E.M. Suh, R.E. Lucas, *et al.* 1999. Subjective well-being: three decades of progress. *Psychol. Bull.* **125**: 276–302.
  39. Kringelbach, M.L. & K.C. Berridge. 2009. Towards a functional neuroanatomy of pleasure and happiness. *Trends Cogn. Sci.* **13**: 479–487.
  40. Diener, E., E. Sandvik & W. Pavot. 2009. Happiness is the frequency, not the intensity, of positive versus negative affect. In *Assessing Well-Being: The Collected Works of Ed Diener*. E. Diener, Ed.: 213–231. Dordrecht: Springer.
  41. Andrews, F.M. & S.B. Withey. 1976. *Social Indicators of Well-Being: Americans' Perceptions of Life Quality*. New York, NY: Plenum Press.
  42. Michalos, A.C. 1985. Multiple discrepancies theory (MDT). *Soc. Indic. Res.* **16**: 347–413.
  43. Veenhoven, R. 2015. Informed pursuit of happiness: what we should know, do know and can get to know. *J. Happiness Stud.* **16**: 1035–1071.
  44. Mendl, M., O.H.P. Burman, R.M.A. Parker, *et al.* 2009. Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. *Appl. Anim. Behav. Sci.* **118**: 161–181.
  45. Carver, C.S. & T.L. White. 1994. Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: the BIS/BAS scales. *J. Pers. Soc. Psychol.* **67**: 319.
  46. DeNeve, K.M. 1999. Happy as an extraverted clam? The role of personality for subjective well-being. *Curr. Dir. Psychol.* **8**: 141–144.
  47. Grinde, B. 2012. *The Biology of Happiness*. Dordrecht: Springer.
  48. Spruijt, B.M., R. van den Bos & F.T. Pijlman. 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.
  49. Diener, E. & M.E. Seligman. 2002. Very happy people. *Psychol. Sci.* **13**: 81–84.
  50. Rojas, M. & R. Veenhoven. 2013. Contentment and affect in the estimation of happiness. *Soc. Indic. Res.* **110**: 415–431.
  51. Trimmer, P.C., E.S. Paul, M.T. Mendl, *et al.* 2013. On the evolution and optimality of mood states. *Behav. Sci.* **3**: 501–521.
  52. Fredrickson, B.L. 2013. Updated thinking on positivity ratios. *Am. Psychol.* **68**: 814–822.
  53. Veenhoven, R. 2013. The four qualities of life ordering concepts and measures of the good life. In *The Exploration of Happiness*. A. Delle Fave, Ed.: 195–226. Dordrecht: Springer.
  54. Clore, G.L. & J. Palmer. 2009. Affective guidance of intelligent agents: how emotion controls cognition. *Cogn. Sys. Res.* **10**: 21–30.
  55. LeDoux, J.E. 2012. Evolution of human emotion: a view through fear. *Prog. Brain Res.* **195**: 431–442.
  56. Fraser, D. 2003. Assessing animal welfare at the farm and group level: the interplay of science and values. *Anim. Welf.* **12**: 433–443.
  57. Dawkins, M.S. 2000. Animal minds and animal emotions. *Am. Zool.* **40**: 883–888.
  58. Mendl, M. & E.S. Paul. 2004. Consciousness, emotion and animal welfare: insights from cognitive science. *Anim. Welf.* **13**: 17–25.
  59. Hewson, C.J. 2003. What is animal welfare? Common definitions and their practical consequences. *Can. Vet. J.* **44**: 496.
  60. Ngamaba, K.H., M. Panagioti & C.J. Armitage. 2017. How strongly related are health status and subjective well-being? Systematic review and meta-analysis. *Eur. J. Public Health* **27**: 879–885.
  61. Lyubomirsky, S., L. King & E. Diener. 2005. The benefits of frequent positive affect: does happiness lead to success? *Psychol. Bull.* **131**: 803–855.
  62. Barak, Y. 2006. The immune system and happiness. *Autoimmun. Rev.* **5**: 523–527.
  63. Schultz, I. 2014. The happiness of babies. A research synthesis. Paper in context of a research internship. Erasmus University Rotterdam.
  64. Lawrence, A.B., R.C. Newberry & M. Špinka. 2018. Positive welfare: what does it add to the debate over pig welfare? *Adv. Pig Welf.* 415–444. <https://doi.org/10.1016/B978-0-08-101012-9.00014-9>.
  65. Simonsen, H.B. 1996. Assessment of animal welfare by a holistic approach: behaviour, health and measured opinion. *Acta Agric. Scand. Sect. A Anim. Sci.* **27**: 91–96.
  66. McMillan, F.D. 2003. Maximizing quality of life in III animals. *J. Am. Anim. Hosp. Assoc.* **39**: 227–235.
  67. McMillan, F.D. 2005. The concept of quality of life in animals. In *Mental Health and Well-Being in Animals*. F.D. McMillan, Ed.: 181–200. Oxford: Blackwell Publishing Ltd.
  68. Yeates, J.W. & D.C.J. Main. 2008. Assessment of positive welfare: a review. *Vet. J.* **175**: 293–300.
  69. Duncan, I.J.H. 1996. Animal welfare defined in terms of feelings. *Acta Agric. Scand. Sect. A Anim. Sci.* **27**: 29–35.
  70. Wiseman-Orr, M.L., E.M. Scott, J. Reid, *et al.* 2006. Validation of a structured questionnaire as an instrument to measure chronic pain in dogs on the basis of effects on health-related quality of life. *Am. J. Vet. Res.* **67**: 1826–1836.
  71. Hughes, B.O. & I.J.H. Duncan. 1988. The notion of ethological need, models of motivation and animal-welfare. *Anim. Behav.* **36**: 1696–1707.
  72. Matthews, L.R. & J. Ladewig. 1994. Environmental requirements of pigs measured by behavioural demand functions. *Anim. Behav.* **47**: 713–719.
  73. Søndergaard, E., M.B. Jensen & C.J. Nicol. 2011. Motivation for social contact in horses measured by operant conditioning. *Appl. Anim. Behav. Sci.* **132**: 131–137.
  74. Pedersen, L.J., L. Holm, M.B. Jensen, *et al.* 2005. The strength of pigs' preferences for different rooting materials measured using concurrent schedules of reinforcement. *Appl. Anim. Behav. Sci.* **94**: 31–48.

75. Webb, L.E., M.B. Jensen, B. Engel, *et al.* 2014. Chopped or long roughage: what do calves prefer? Using cross point analysis of double demand functions. *PLoS One* **9**: e88778.
76. Held, S.D.E. & M. Špinka. 2011. Animal play and animal welfare. *Anim. Behav.* **81**: 891–899.
77. Ahloy-Dallaire, J., J. Espinosa & G. Mason. 2017. Play and optimal welfare: does play indicate the presence of positive affective states? *Behav. Process.* <https://doi.org/10.1016/j.beproc.2017.11.011>.
78. Spijkerboer, A., E. Utens, A. Bogers, *et al.* 2008. Long-term behavioural and emotional problems in four cardiac diagnostic groups of children and adolescents after invasive treatment for congenital heart disease. *Int. J. Cardiol.* **125**: 66–73.
79. Sheffler, L.C., C. Hanley, A. Bagley, *et al.* 2009. Comparison of self-reports and parent proxy-reports of function and quality of life of children with below-the-elbow deficiency. *J. Bone Joint Surg.* **91**: 2852–2859.
80. Noelle-Neuman, E. 1977. Die Lage der Forschung an den Universitäten. Erster Bericht über die Ergebnisse einer Repräsentativumfrage unter 5000 Hochschullehrern Assistenten und Doktoranden. *Forstarchiv* **48**: 236–241.
81. Diener, E. & M.Y. Chan. 2011. Happy people live longer: subjective well-being contributes to health and longevity. *Appl. Psychol. Health Well-Being* **3**: 1–43.
82. Steptoe, A., J. Wardle & M. Marmot. 2005. Positive affect and health-related neuroendocrine, cardiovascular, and inflammatory processes. *Proc. Natl. Acad. Sci. USA* **102**: 6508–6512.
83. Rosenkranz, M.A., D.C. Jackson, K.M. Dalton, *et al.* 2003. Affective style and in vivo immune response: neurobehavioral mechanisms. *Proc. Natl. Acad. Sci. USA* **100**: 11148–11152.
84. Sin, N.L., J.E. Graham-Engeland & D.M. Almeida. 2015. Daily positive events and inflammation: findings from the National Study of Daily Experiences. *Brain Behav. Immun.* **43**: 130–138.
85. Seeman, T.E., B.S. McEwen, J.W. Rowe, *et al.* 2001. Allostatic load as a marker of cumulative biological risk: MacArthur studies of successful aging. *Proc. Natl. Acad. Sci. USA* **98**: 4770–4775.
86. Seeman, T.E., B.H. Singer, J.W. Rowe, *et al.* 1997. Price of adaptation—allostatic load and its health consequences: MacArthur studies of successful aging. *Arch. Intern. Med.* **157**: 2259–2268.
87. Juster, R.-P., B.S. McEwen & S.J. Lupien. 2010. Allostatic load biomarkers of chronic stress and impact on health and cognition. *Neurosci. Biobehav. Rev.* **35**: 2–16.
88. Schenk, H.M., B.F. Jeronimus, L. van der Krieke, *et al.* 2018. Associations of positive affect and negative affect with allostatic load: a lifelines cohort study. *Psychosom. Med.* **80**: 160–166.
89. Berridge, K.C. & M.L. Kringelbach. 2015. Pleasure systems in the brain. *Neuron* **86**: 646–664.
90. Lindquist, K.A., A.B. Satpute, T.D. Wager, *et al.* 2015. The brain basis of positive and negative affect: evidence from a meta-analysis of the human neuroimaging literature. *Cereb. Cortex* **26**: 1910–1922.
91. Schmaal, L., D.J. Veltman, T.G. van Erp, *et al.* 2016. Subcortical brain alterations in major depressive disorder: findings from the ENIGMA Major Depressive Disorder working group. *Mol. Psychiatry* **21**: 806.
92. Urry, H.L., J.B. Nitschke, I. Dolski, *et al.* 2004. Making a life worth living: neural correlates of well-being. *Psychol. Sci.* **15**: 367–372.
93. Davidson, R.J. 2002. Toward a biology of positive affect and compassion. In *Visions of Compassion: Western Scientists and Tibetan Buddhists Examine Human Nature*. R.J. Davidson & A. Harrington, Eds.: 107–130. New York, NY: Oxford University Press.
94. Davidson, R.J., D.C. Jackson & N.H. Kalin. 2000. Emotion, plasticity, context, and regulation: perspectives from affective neuroscience. *Psychol. Bull.* **126**: 890.
95. Kong, F., S. Hu, X. Wang, *et al.* 2015. Neural correlates of the happy life: the amplitude of spontaneous low frequency fluctuations predicts subjective well-being. *Neuroimage* **107**: 136–145.
96. Radley, J., D. Morilak, V. Viau, *et al.* 2015. Chronic stress and brain plasticity: mechanisms underlying adaptive and maladaptive changes and implications for stress-related CNS disorders. *Neurosci. Biobehav. Rev.* **58**: 79–91.
97. De Neve, J.-E. 2011. Functional polymorphism (5-HTTLPR) in the serotonin transporter gene is associated with subjective well-being: evidence from a US nationally representative sample. *J. Hum. Genet.* **56**: 456.
98. Epel, E.S., E.H. Blackburn, J. Lin, *et al.* 2004. Accelerated telomere shortening in response to life stress. *Proc. Natl. Acad. Sci. USA* **101**: 17312–17315.
99. Archer, T. 2017. Health benefits for ageing: positive affect and life satisfaction, exercise and coping, and telomere length. *J. Ment. Health Aging* **1**: 13–17.
100. Zhou, L. & J.A. Foster. 2015. Psychobiotics and the gut-brain axis: in the pursuit of happiness. *Neuropsychiatr. Dis. Treat.* **11**: 715.
101. Csikszentmihalyi, M. & R. Larson. 2014. Validity and reliability of the experience-sampling method. In *Flow and the Foundations of Positive Psychology* 35–54. Springer.
102. Kahneman, D., A.B. Krueger, D.A. Schkade, *et al.* 2004. A survey method for characterizing daily life experience: the day reconstruction method. *Science* **306**: 1776–1780.
103. Steptoe, A., K. O'donnell, E. Badrick, *et al.* 2007. Neuroendocrine and inflammatory factors associated with positive affect in healthy men and women: the Whitehall II study. *Am. J. Epidemiol.* **167**: 96–102.
104. Murphy, E., R.E. Nordquist & F.J. van der Staay. 2014. A review of behavioural methods to study emotion and mood in pigs. *Sus scrofa. Appl. Anim. Behav. Sci.* **159**: 9–28.
105. Makowska, I.J. & D.M. Weary. 2013. Assessing the emotions of laboratory rats. *Appl. Anim. Behav. Sci.* **148**: 1–12.
106. Mitsui, S., M. Yamamoto, M. Nagasawa, *et al.* 2011. Urinary oxytocin as a noninvasive biomarker of positive emotion in dogs. *Horm. Behav.* **60**: 239–243.
107. Reimert, I., J.E. Bolhuis, B. Kemp, *et al.* 2013. Indicators of positive and negative emotions and emotional contagion in pigs. *Physiol. Behav.* **109**: 42–50.

108. Harding, E.J., E.S. Paul & M. Mendl. 2004. Animal behaviour: cognitive bias and affective state. *Nature* **427**: 312–312.
109. Lee, C., E. Verbeek, R. Doyle, *et al.* 2016. Attention bias to threat indicates anxiety differences in sheep. *Biol. Lett.* **12**. <https://doi.org/10.1098/rsbl.2015.0977>.
110. Webb, L.E., B. Engel, K. van Reenen, *et al.* 2017. Barren diets increase wakeful inactivity in calves. *Appl. Anim. Behav. Sci.* **197**: 9–14.
111. Reefmann, N., B. Wechsler & L. Gyax. 2009. Behavioural and physiological assessment of positive and negative emotion in sheep. *Anim. Behav.* **78**: 651–659.
112. Mormède, P., S. Andanson, B. Auperin, *et al.* 2007. Exploration of the hypothalamic–pituitary–adrenal function as a tool to evaluate animal welfare. *Physiol. Behav.* **92**: 317–339.
113. Logan, R.W., N. Edgar, A.G. Gillman, *et al.* 2015. Chronic stress induces brain region-specific alterations of molecular rhythms that correlate with depression-like behavior in mice. *Biol. Psychiatry* **78**: 249–258.
114. Koolhaas, J.M., A. Bartolomucci, B. Buwalda, *et al.* 2011. Stress revisited: a critical evaluation of the stress concept. *Neurosci. Biobehav. Rev.* **35**: 1291–1301.
115. Kelly, J.R., Y. Borre, C. O'Brien, *et al.* 2016. Transferring the blues: depression-associated gut microbiota induces neurobehavioural changes in the rat. *J. Psychiatr. Res.* **82**: 109–118.
116. Shivel, C.A. & S.L. Willard. 2012. Behavioral and neurobiological characteristics of social stress versus depression in nonhuman primates. *Exp. Neurol.* **233**: 87–94.
117. Asher, L., M. Friel, K. Griffin, *et al.* 2016. Mood and personality interact to determine cognitive biases in pigs. *Biol. Lett.* **12**: 1–4.
118. Bateson, M. & D. Nettle. 2015. Development of a cognitive bias methodology for measuring low mood in chimpanzees. *PeerJ* **3**: e998.
119. Doyle, R.E., S. Vidal, G.N. Hinch, *et al.* 2010. The effect of repeated testing on judgement biases in sheep. *Behav. Process.* **83**: 349–352.
120. Bethell, E.J. & N.F. Koyama. 2015. Happy hamsters? Enrichment induces positive judgement bias for mildly (but not truly) ambiguous cues to reward and punishment in *Mesocricetus auratus*. *R. Soc. Open Sci.* **2**: 17.
121. Puppe, B., K. Ernst, P.C. Schon, *et al.* 2007. Cognitive enrichment affects behavioral reactivity in domestic pigs. *Appl. Anim. Behav. Sci.* **105**: 75–86.
122. Pomerantz, O. & J. Terkel. 2009. Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **71**: 687–695.
123. Zebunke, M., J. Langbein, G. Manteuffel, *et al.* 2011. Autonomic reactions indicating positive affect during acoustic reward learning in domestic pigs. *Anim. Behav.* **81**: 481–489.
124. Fureix, C., C. Beaulieu, S. Argaud, *et al.* 2015. Investigating anhedonia in a non-conventional species: do some riding horses *Equus caballus* display symptoms of depression? *Appl. Anim. Behav. Sci.* **162**: 26–36.
125. Rochais, C., S. Henry, C. Fureix, *et al.* 2016. Investigating attentional processes in depressive-like domestic horses (*Equus caballus*). *Behav. Process.* **124**: 93–96.
126. Burman, O.H.P., R.M.A. Parker, E.S. Paul, *et al.* 2008. Sensitivity to reward loss as an indicator of animal emotion and welfare. *Biol. Lett.* **4**: 330–333.
127. Meagher, R.K. & G.J. Mason. 2012. Environmental enrichment reduces signs of boredom in caged mink. *PLoS One* **7**: e49180.
128. King, J.E. & V.I. Landau. 2003. Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *J. Res. Person.* **37**: 1–15.
129. Robinson, L.M., N.K. Waran, M.C. Leach, *et al.* 2016. Happiness is positive welfare in brown capuchins (*Sapajus apella*). *Appl. Anim. Behav. Sci.* **181**: 145–151.
130. Gartner, M.C., D.M. Powell & A. Weiss. 2016. Comparison of subjective well-being and personality assessments in the clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and African lion (*Panthera leo*). *J. Appl. Anim. Welf. Sci.* **19**: 294–302.
131. Weiss, A., M.J. Adams & J.E. King. 2011. Happy orang-utans live longer lives. *Biol. Lett.* **23**: 872–874.
132. Wemelsfelder, F. 2007. How animals communicate quality of life: the qualitative assessment of behavior. *Anim. Welf.* **16**: 25.
133. Wemelsfelder, F., E.A. Hunter, M.T. Mendl, *et al.* 2000. The spontaneous qualitative assessment of behavioral expressions in pigs: first explorations of a novel methodology for integrative animal welfare measurement. *Appl. Anim. Behav. Sci.* **67**: 193–215.
134. Brscic, M., F. Wemelsfelder, E. Tessitore, *et al.* 2009. Welfare assessment: correlations and integration between a qualitative behavioral assessment and a clinical/health protocol applied in veal calves farms. *Ital. J. Anim. Sci.* **8**: 601–603.
135. Bokkers, E., M. de Vries, I. Antonissen, *et al.* 2012. Inter- and intra-observer reliability of experienced and inexperienced observers for the qualitative behavior assessment in dairy cattle. *Anim. Welf.* **21**: 307–318.
136. Smith, R.F. & H. Dobson. 2002. Hormonal interactions within the hypothalamus and pituitary with respect to stress and reproduction in sheep. *Domest. Anim. Endocrinol.* **23**: 75–85.
137. Segner, H., H. Sundh, K. Buchmann, *et al.* 2012. Health of farmed fish: its relation to fish welfare and its utility as welfare indicator. *Fish Physiol. Biochem.* **38**: 85–105.
138. Korte, S.M., B. Olivier & J.M. Koolhaas. 2007. A new animal welfare concept based on allostasis. *Physiol. Behav.* **92**: 422–428.
139. Bateson, M. 2016. Cumulative stress in research animals: telomere attrition as a biomarker in a welfare context? *Bioessays* **38**: 201–212.
140. Briefer, E. 2012. Vocal expression of emotions in mammals: mechanisms of production and evidence. *J. Zool.* **288**: 1–20.
141. Brudzynski, S.M. 2013. Ethotransmission: communication of emotional states through ultrasonic vocalization in rats. *Curr. Opin. Neurobiol.* **23**: 310–317.
142. Knutson, B., J. Burgdorf & J. Panksepp. 2002. Ultrasonic vocalizations as indices of affective states in rats. *Psychol. Bull.* **128**: 961.

143. Portfors, C.V. 2007. Types and functions of ultrasonic vocalizations in laboratory rats and mice. *J. Am. Assoc. Lab. Anim. Sci.* **46**: 28–34.
144. Panksepp, J. & J. Burgdorf. 2000. 50-kHz chirping (laughter?) in response to conditioned and unconditioned tickle-induced reward in rats: effects of social housing and genetic variables. *Behav. Brain Res.* **115**: 25–38.
145. Burgdorf, J., J. Panksepp & J.R. Moskal. 2011. Frequency-modulated 50 kHz ultrasonic vocalizations: a tool for uncovering the molecular substrates of positive affect. *Neurosci. Biobehav. Rev.* **35**: 1831–1836.
146. Stomp, M., M. Leroux, M. Cellier, *et al.* 2018. An unexpected acoustic indicator of positive emotions in horses. *PLoS One* **13**: e0197898.
147. Finlayson, K., J.F. Lampe, S. Hintze, *et al.* 2016. Facial indicators of positive emotions in rats. *PLoS One* **11**: e0166446.
148. Waller, B.M. & J. Micheletta. 2013. Facial expression in nonhuman animals. *Emot. Rev.* **5**: 54–59.