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### Review

### Animal welfare: At the interface between science and society

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### ABSTRACT

The general concept of animal welfare embraces a continuum between negative/bad welfare and positive/good welfare. Early approaches to defining animal welfare were mainly based on the exclusion of negative states, neglecting the fact that during evolution animals optimised their ability to interact with and adapt to their environment(s). An animal's welfare status might best be represented by the adaptive value of the individual's interaction with a given environmental setting but this dynamic welfare concept has significant implications for practical welfare assessments.

Animal welfare issues cannot simply be addressed by means of objective biological measurements of an animal's welfare status under certain circumstances. In practice, interpretation of welfare status and its translation into the active management of perceived welfare issues are both strongly influenced by context and, especially, by cultural and societal values. In assessing whether or not a given welfare status is morally acceptable, animal welfare scientists must be aware that scientifically based, operational definitions of animal welfare will necessarily be influenced strongly by a given society's moral understanding.

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### Introduction

Social and political interest in animal welfare and welfare management has increased substantially in recent years (see, for example, Bayvel and Cross, 2010; Ingenbleek and Immink, 2010). Animal welfare scientists have been given the task of defining objective and quantifiable parameters of an animal's welfare status under given conditions and providing solutions to animal welfare problems identified by society. However, there is no consensus on how to measure the welfare status of an animal objectively or the welfare implications of any given management practice. Moreover, every definition of animal welfare is influenced by the moral or ethical standards of society. We must therefore recognise that objectivity in analysis cedes inevitably to the subjectivity of ethical assessment when determining whether a welfare status is or is not 'acceptable' to society. Thus the 'translation' of welfare assessments into management practice and the way in which that management practice is viewed by society are both affected markedly by public understanding and public attitudes.

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### Ethical contexts for considerations on animal welfare

The political relevance of animal welfare science is strongly (if not exclusively) based on societal concerns about how animals are treated. Whatever a society's view on the *importance* of animal welfare, the interpretation and moral evaluation of what constitutes welfare or, more importantly, welfare problems, differs between cultures, regions, time, and individuals (Stafleu et al., 1996; Cohen et al., 2009; Yeates, 2010). Moreover, a person's values may change depending on the context (Kupper, 2009). For example, the value of a mouse may depend on whether it is considered a companion or laboratory animal or a pest. That said, as Webster (1994) argued: 'a rat is a rat whether we define it as vermin or as a pet'.

In order to deliver solutions to perceived welfare issues, animal welfare scientists must take their scientifically based considerations into account and the recommendations they make regarding animal welfare issues must comply with the moral values of society in order to generate sustainable approaches to animal welfare management. A systematic approach is needed to identify potential moral dilemmas in animal welfare and factors that might, influence these dilemmas. The Dutch Animal Welfare Council<sup>1</sup> recently developed such an approach, the so-called ethical framework (Fig. 1), to structure discussions about the ethical dimension of

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<sup>&</sup>lt;sup>1</sup> Raad voor Dierenaangelegenheden (RDA).

### Framework: ethical consideration on animal welfare Based on: Fundamental moral questions E.g. do we have the moral duty to take care Societal moral of animal welfare? Broadly accepted and based on: Intuition/feelings (e.g. perception of animal welfare) Do such potential duties result in moral Principles (e.g. intrinsic value, conflicts that are related to animal welfare? autonomy, justice) Facts (being confronted with suffering If so, how should we deal with welfareanimals) related moral conflicts? and Scientific knowledge on Specific considerations, such as: (relevant and actual, e.g.) Are our moral duties to take care of animal **Emotion & Cognition** welfare depending on the specific context/ **Economic interests** objective, within which we are confronted Environment with these animals? Human-animal relation Should suffering and stress of animals be Education prevented at all times or are they Nature acceptable under certain conditions? Domestication Is evidence of the animals' ability to perceive its own emotional state a **Evolution** prerequisite for our moral duty to take care of the animals' welfare? interests are weighed

Fig. 1. The aim of this framework (adopted from RDA, 2010) is to structure discussions about the ethics of current and possible future animal welfare issues. Such discussions should cover what we should do from a moral perspective in any given situation, identify relevant ethical issues, specifically in relation to animal welfare, and outline the steps that need to be taken to resolve these issues.

current and potential future animal welfare issues (RDA, 2010). Such a discussion should cover what needs to be done from a moral perspective in any given situation, identify relevant ethical issues (specifically in relation to animal welfare) and outline the steps that need to be taken to resolve these issues.

It should be clear that such a framework is intended to identify relevant ethical issues and potential moral dilemmas rather than to yield straightforward solutions. Furthermore, the results of these considerations will not be universally valid but will differ significantly between societies. The importance of such a framework however is that it provides a basis for discussion of animal welfare within a given society.

# Welfare: Approaching a scientific definition of a complex concept

An example of the struggle to find an operational definition for a complex concept may be found in the development of the concept of 'health'. Whilst health was initially defined as the absence of disease or infirmity, the current WHO<sup>2</sup> definition is 'Health is a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity' (WHO, 1946). Thus, 'health' is positioned at the positive end of the continuum between illness and well-being. This WHO definition has not been altered for over 60 years, but still leads to controversial discussion (Jadad and O'Grady, 2008). Some have even argued that this is 'a ludicrous definition that would leave

most of us unhealthy most of the time' (Smith, 2008). A comparable development can be observed in the discussion about welfare concepts.

The general concept of animal welfare recognises that, at any one point in time, an animal's welfare status lies on the continuum between negative/bad welfare (i.e. suffering) (see, for example, Dawkins, 2008) and positive/good welfare (i.e. well-being) (see, for example, Yeates and Main, 2008). Regardless of how the animal's actual welfare status might be assessed from its behaviour or response to environmental stimuli, early approaches to the interpretation of positive or acceptable animal welfare were often based almost entirely on the simple exclusion of negative attributes and states. Thus, positive welfare was defined as the absence of being injured or in some way compromised; in other words, the absence of suffering. Today, welfare scientists increasingly consider the presence of actual 'positive states' to be relevant to well-being (Yeates and Main, 2008).

This emphasis on the avoidance of negative states or conditions influenced one of the first attempts to define positive welfare. The Brambell Committee<sup>3</sup> proposed that (positive) animal welfare is preserved if the animals are kept free from:

- hunger, thirst or inadequate food;
- thermal and physical discomfort;

<sup>&</sup>lt;sup>2</sup> World Health Organisation (WHO).

<sup>&</sup>lt;sup>3</sup> Brambell Committee: A technical committee set up by the UK Government in 1965 to inquire into the welfare of animals kept under intensive livestock husbandry systems.

- injuries or diseases;
- fear and chronic stress, and were
- free to display normal, species-specific behavioural patterns.

The first four of what became known as *the five freedoms* were formulated from the perspective that the absence of negative states ensures welfare; only the fifth freedom, although more indirectly, implied that positive aspects contributed to welfare. Today, the five freedoms are broadly used as a guideline for welfare assessment protocols, with the welfare state of an animal being characterised as unimpaired if it complies with the five freedoms.

These five freedoms were primarily derived in relation to the welfare of farm animals, and, with the exception of the fifth freedom, would appear to consider that animals are passive within their environment. As a result, the concept may be of only limited use when applied to the assessment of welfare in animals whose environment is less rigorously controlled by human intervention, such as wild, or free-range animals. The five freedoms ignore the fact that (except in the specific instances where natural selection has been largely counteracted or manipulated by humans) animals have evolved, optimising the ability to interact with and adapt to (changing conditions within) their environment. Perhaps the first four freedoms might be better re-cast by replacing the rather negative 'freedom from' by the more positive 'freedom to react to...', in order to integrate the first four freedoms with our understanding of an individual animal's ability to adapt.

## Positive welfare: Characterised by the absence of negative stimuli and negative emotions?

Considering the importance of an animal's ability to adapt to a given situation, it is debatable whether freedom from negative influences or stimuli alone necessarily ensures the animal's welfare. It is broadly accepted that pain (see, for example, Rutherford, 2002) and anxiety (see, Mendl et al., 2010) compromise welfare. However, this ignores the biological function of a so-called 'negative' emotional reaction, which evolved specifically to protect an individual's overall welfare. For example, a stimulus inducing fear or anxiety most likely evokes avoidance (see, for example, Ennaceur et al., 2006), or risk assessment behaviour (see, Rodgers et al., 1997) that protects the individual from being harmed. Thus a negative emotional reaction should be considered as an indicator of an animal's adaptive capacity to avoid 'negative' welfare. Likewise, 'negative' stimuli are a necessary part of the normal behavioural experience in order to establish and maintain stable social relations. Threat behaviour, for example, is likely to elicit fear in the recipient of this behaviour, but at the same time is part of a complex behavioural repertoire, which has evolved to avoid/suppress more direct harmful aggression between social partners (Mendl and Deag, 1995).

From the above, it can be concluded that the five freedoms presented by Professor Brambell and his Committee may actually contradict each other. The general absence of 'negative' stimuli prevents the expression of an individual's 'natural' behavioural repertoire, for example avoidance behaviour and risk assessment behaviour, the establishment of a stable social hierarchy, or the occupancy of a territory that needs to be defended against intruders. Rather than excluding potentially negative stimuli from the individual animal's experience, the freedom to express a full range of natural behaviour requires that the animal has the freedom to react appropriately to a potentially harmful (negative) stimulus. Consequently, animal welfare will be compromised if an individual is not given the possibility to react adequately to such negative stimuli, that is, to escape from or avoid potential harm or threat, or, as Webster (1994) puts it 'the welfare of an animal is determined by its capacity to avoid suffering and sustain fitness'.

Veissier and Boissy (2007) argue that 'stress and welfare are opposites, related to the mental states of individuals' with 'welfare being higher for positive expectation and lower for negative or uncertain expectations'. There is, however, a broad range of naturally occurring situations in which an individual animal actively chooses to expose itself to a stressful situation, for example when exploring a novel environment. The ability to cope with environmental challenges requires the use of the individual's full emotional and behavioural repertoire, including those aspects that are usually regarded as 'negative'.

On the basis of these considerations, we might redefine and refine the Brambell Committee's original welfare concept to suggest that positive welfare depends on the freedom to *react appropriately* and adequately to

- hunger, thirst or incorrect food;
- thermal and physical discomfort;
- injuries or diseases;
- fear and chronic stress, and thus,
- the freedom to display normal, species-specific behavioural patterns and *adapt to changing living conditions*.

This more dynamic concept, however, still leaves out the appreciation of positive emotions.

### Welfare as a positive emotional state as perceived by the animal?

As an extension to the assessment of 'negative' welfare (i.e. suffering), newer approaches have been directed towards the identification of indicators of 'positive' welfare (Yeates and Main, 2008) or well-being (Wojciechowska and Hewson, 2005). According to Duncan (1993a,b, 1996) 'welfare is about both positive and negative emotions, and therefore about the satisfaction of needs and desires'. Following this line of reasoning, Mench and Duncan (1998) stated that the concept of welfare assumes the presence of positive and negative emotions, not only the absence of suffering. More recently. Bracke and Hopster (2006) argued that positive welfare was indicated by natural behaviour, with the latter being defined as 'pleasurable and promoting biological functioning'. This, however, might lead to the somewhat misleading conclusion that the only natural state is a pleasurable one. As already outlined above, there may be little doubt that a variety of non-pleasurable states, such as fear- and defence-related states, are natural and are of biological relevance.

Welfare concepts have now been extended to include the animal's own perceptions. For example, Bracke et al. (1999) state: 'Animal welfare is the quality of life as perceived by the animal itself'. These and similar concepts take into consideration current knowledge of animal consciousness that assumes that vertebrates (and some invertebrates) not only experience emotions momentarily, but that they are able to relate them to contexts and experiences, and therefore possess a certain emotional adaptability (Myers, 1992; Myers and Diener, 1995; Duncan, 1993, 1996; Dawkins, 1998; Paul et al., 2005; Boissy et al., 2007; Ohl and Hellebrekers, 2009; Broom, 2010; Mendl et al., 2010). In line with these considerations, the human health-related concept of quality of life, which is strongly focused on how an individual subjectively perceives life at any one point in time, could be relevant to animal welfare (Taylor and Mills, 2007). The relevance of positive emotions for the concept of animal welfare might lead to a further modification of the Brambell Committee's five freedoms to suggest that positive welfare depends on the freedom adequately to react to:

- hunger, thirst or incorrect food;
- thermal and physical discomfort;

- injuries or diseases;
- fear and chronic stress, and so
- the freedom to display normal, species-specific behavioural patterns and adapt to changing living conditions up to a level that is perceived as positive.

In all these analyses, welfare is considered exclusively at a state level (that is, in response to a distinct stimulus or pattern of stimuli at a given point in time). As a measure of biological function, welfare, in our opinion, should not be considered a static concept, but should take into account the dynamics of the individual's interaction with its environment over time.

### Welfare as a function of adaptation

Approaches to more biologically based welfare concepts generally include the process of adaptation. Korte et al. (2007) suggested focusing on an animal's ability to adapt to changing environmental conditions (allostasis) to define its welfare status. In this concept, an animal's welfare is not threatened as long as it is able to meet environmental challenges, i.e. 'when the regulatory range of allostatic mechanisms matches the environmental demands' (Korte et al., 2007).

Others state that situations that exceed an individual's adaptive capacity may result in conditions (even pathological conditions) that lack adaptive value and consequently compromise welfare (Ohl et al., 2008; Salomons et al., 2009). Barnard and Hurst (1996) advocated a welfare concept based on the Environment of Evolutionary Adaptation' (EEA) proposing that 'welfare can be interpreted only in terms of what natural selection has designed an organism to do and how circumstances impinge on its functional design'. Following the idea that species-specific 'decision rules' evolved in response to environmental conditions, Barnard and Hurst (1996) hypothesized that this repertoire did not change significantly during the (relatively short from an evolutionary perspective) period of domestication. From this point of view, selective breeding in domestic animals, often to obtain specific physiological/anatomical characteristics such as higher performance (meat/eggs etc.), carries the risk that the animal's adaptive capacity will become impaired (as conflicting with decision rules) rather than being an adaptive process in itself as has been argued by others (Jensen, 2010).

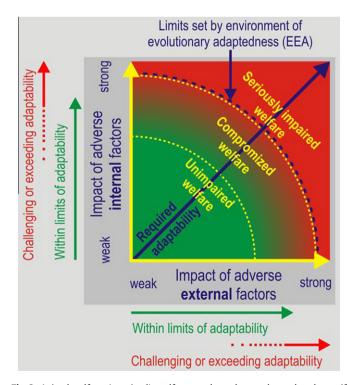
Yet evolutionary processes can emerge quite rapidly, within several dozens instead of several hundreds of generations (Irons, 1998; Shimada et al., 2010), with strain- and breed-specific changes occurring in physiological/anatomical characteristics (Inoue-Murayama, 2009; Benjamini et al., 2010; Groeneveld et al., 2010). Irons (1998) hypothesized that 'environmental novelties have quite specific effects, disrupting some [characteristics] but not others', which essentially would mean that a given environmental pressure would be more likely to alter those characteristics that are relevant to that particular environmental stimulus than to alter the species-specific repertoire as a whole. He therefore suggests thinking in terms of an 'adaptively relevant environment'.

In our view it would be more useful to think in terms of an adaptively relevant subset of the *behavioural repertoire* that may relate to a given environmental situation. Such a distinction, however, is probably semantic, because all aspects of an adaptive repertoire will necessarily influence each other. More importantly, intra-species variation in individual adaptability will develop through ontogenetic processes as a result of specific environmental conditions (Barash, 1997; Piersma and Drent, 2003). Consequently, individual characteristics of adaptability have to be considered as well as any potential species-specific traits.

In such an adaptive concept, the individual animal's welfare may be threatened as the animal approaches the limits of its own adaptability (Fig. 2). As we have outlined above, the adaptive capacity of an animal includes emotional responses, which are usually understood as being 'negative'. However, a lack of adaptation towards aversive stimuli may lead to either sensitisation or generalisation of such stimuli and may ultimately result in dysfunctional, non-adaptive anxiety responses (Salomons et al., 2010). An animal's welfare may thus be compromised if the impact of adverse internal or external factors (or their interaction) challenges the animal's adaptability (Ohl et al., 2008), such that the animal cannot adapt to the demands of the prevailing environmental circumstances to enable it to reach a state which it perceives as positive.

The measurable component of an individual's ability to adapt is its biological functioning within a certain context. An important indicator of an animal's functioning, besides its physical health, is the extent to which it displays adaptive behaviour. Behaviour is strongly context-dependent, because behaviour has evolved as part of animals' capacity to cope with specific environment stimuli. The animal's behavioural response will therefore depend on the context, the species-specific behavioural repertoire, and the individual's adaptability at any given moment. However, it is only the change in response towards a given stimulus over time that will tell us whether an individual is able to adapt to that stimulus. For example, an acute, strong anxiety response towards an unknown stimulus may be followed by rapid adaptation, while a moderate anxiety response may remain unchanged over a prolonged period of time, indicating a lack of adaptive capacity (Salomons et al., 2009).

Thus, for the assessment of the biological aspects of animal welfare, it is more relevant to evaluate the animal's adaptive capacity and whether the demands of the respective environmental circumstances can be fulfilled within the limits of its adaptive capacity, than to establish whether a given situation induces an acute



**Fig. 2.** Animal welfare. An animal's welfare may be endangered or reduced even if the limits of adaptability have not yet been exceeded. The limits of adaptability are set by the environment or evolutionary adaptedness (Barnard and Hurst, 1996), or when the environmental demands exceed the regulatory range of allostatic mechanisms (Korte et al., 2007).

'negative' emotional or physiological state. The relevance of an individual's adaptive capacity to the concept of animal welfare leads to a final modification of the Brambell Committee's five freedoms. So:

An individual is in a positive welfare state when it has the freedom *adequately to react to* 

- hunger, thirst or incorrect food;
- thermal and physical discomfort;
- injuries or diseases;
- fear and chronic stress, and thus,
- the freedom to display normal behavioural patterns that allow the animal to adapt to the demands of the prevailing environmental circumstances and enable it to reach a state that it perceives as positive.

The application of such a dynamic welfare concept based on the adaptive capacity of an individual has significant implications for practical welfare assessments.

## Practical implications at the interface between science and society

Protocols for the assessment of animal welfare mostly comprise a checklist of rather static measures, such as those of the initial Brambell Committee freedoms (as for example the Welfare Quality Project; Knierim and Winckler, 2009), rather than taking into account the relevance of changes in measures over time. Instead of proclaiming that 'negative emotions such as fear, distress, frustration or apathy should be avoided whereas positive emotions such as security or contentment should be promoted' (Knierim and Winckler, 2009), we should direct our attention to determining whether the animal's behaviour allows it to meet the demands of its environmental circumstances and whether the environmental circumstances allow the animal to deploy its needs which may be different, depending on age (ontogenetic phase), reproductive period, or season (see, Dawkins, 1998). In practice, this means that hunger is not necessarily associated with a negative welfare state (D'Eath et al., 2009), provided that the animal is free to react to this state adequately by, for example, expressing foraging behaviour and finding food (Table 1). Welfare, in this example, would only be compromised if the animal was not allowed adequately to react to the circumstances up to a level which it perceives as positive (i.e. foraging and finally finding food) or if its physiological adaptivity were exceeded (not fulfilling nutritional needs).

It should be noted here that selective breeding processes may result in scenarios where the dynamic nature of adaptive processes is compromised. For example, broiler chickens have been selected for rapid growth through virtually unlimited voluntary feed intake (Decuypere et al., 2010). As a result, the birds' feeding behaviour can no longer fulfill the demands of environmental circumstances, as the latter will either result in extreme obesity (if unlimited food is available) or chronic hunger (if food is restricted).

Animal welfare assessments, however, are not only important for closely-managed animals (domestic livestock, domestic pets, or other animals whose environment is strictly controlled by human activity). Welfare issues may also arise in situations in which animals are living more freely, but under human responsibility, such as in nature conservation areas (Blumstein, 2010). Under these 'more natural' living conditions, the broader application of a more dynamic concept for the assessment of animal welfare becomes apparent. For example, natural environmental processes in populations of grazing animals comprise seasonal changes in food availability, resulting by definition in periods of hunger. Temperate grazers, however, have evolved to be able to cope with changing conditions, and their overall welfare will be compromised only if food restriction persists beyond their adaptive capacity (i.e. depletion of their body fat reserve).

Assessment of the welfare of free-range animals challenges the biological relevance of assessment protocols developed for more closely managed animals. The biological reality that natural, environmental processes potentially imply time-limited periods of less positive or even negative welfare conditions often results in a conflict between scientific facts and societal feelings. This recently occurred in The Netherlands, where an intense social and political debate developed around the welfare of free-ranging grazers in a nature conservation area, the 'Oostvaardersplassen'. To maintain open shallow pools and grass lawns as feeding ground for wetland

**Table 1**The Welfare Quality Project has been developed for application to animals whose environment is controlled by human management. To assess animal welfare more widely (including the welfare of wild, or free-ranging animals) the fact has to be taken into account that animals have evolved to optimise their ability to interact with and adapt to its circumstances. Thus, a more dynamic concept referring to the individual animal's ability to adapt is necessary.

Criteria for animal welfare		
Static and depending on strictly managed environmental circumstances (adopted from Welfare Quality Project; Blokhuis et al., 2008)		Dynamic and referring to the individual's adaptive capacities
Animals should not suffer from prolonged hunger Animals should not suffer from prolonged thirst	Good feeding	The animal should be free adequately to react to hunger/thirst, e.g. to perform foraging behaviour and find appropriate food and water.
Animals should be comfortable, especially within their lying areas Animals should be in a good thermal environment Animals should be able to move around freely	Good housing	The animals should be free adequately to react to climate conditions, e.g. find shelter when needed
Animals should not be physically injured  Animals should be free of disease  Animals should not suffer from pain induced by inappropriate	Good health	The animals should be free adequately to react to physical injury or disease, e.g. find rest and shelter  Management should provide the animal with an environment allowing the animal to adapt to the demands of the prevailing environmental circumstances
management		
Animals should be allowed to express natural, non-harmful, social behaviour	Appropriate behaviour	The animal should be free to express its full behavioural repertoire
Animals should have the possibility of expressing other intuitively desirable natural behaviours, such as exploration and play		The animal should be free adequately to respond to social interactions
Good humane-animal relationships are beneficial to the welfare of animals  Animals should not experience negative emotions such as fear, distress, frustration or apathy		The animal should be free to experience the full spectrum of emotional states and respond to those states adequately

birds, populations of primitive breeds of cattle and horses were introduced in 1983 and 1984, and red deer in 1992. Populations are unmanaged (except for the humane destruction of animals in extremis) and entirely self-sustaining. However, with time, the large herbivore species were considered part of the ecosystem rather than a natural way to manage the grasslands. This shift in attitude has brought managers into conflict with the wider Dutch public, which feels that society has some responsibility for the welfare of these animals, which were introduced in the first place by human agency. Specifically, the question arose whether prolonged food-restriction due to poor grazing conditions during a long cold winter, led to unnecessary suffering in these animals and constituted a welfare issue.

From a scientific point of view, most temperate ungulates pass through periods of food abundance and shortage at different times of year – and are indeed well adapted to counteract any shortfall in food intake in seasons of shortage by mobilising fat reserves deposited during periods of comparative abundance (McEwen et al., 1957; Kay, 1979). Thus a diminished energy intake relative to energy demand should not necessarily be considered to compromise welfare since the animal has adapted to deal with such an imbalance. However, the Dutch public strongly feels that managers are morally obliged to take all necessary measures to minimise the perceived unnecessary suffering of these animals. In this example, much depends of course on the definition of what is or is not considered 'unnecessary suffering' and, perhaps, what constitutes wild, or ultimately man-managed populations. It is notable that one major aspect of this debate seemed to be the question whether criteria used for welfare assessment in freely living animals are different from those used in animals managed more closely (KNMvD, 2010).4

The sometimes heated debate on this issue was sufficient to prompt the Dutch Government to convene a special committee of international scientists to clarify the basis of this conflict between science and society, and to suggest appropriate management measures to resolve any possible welfare issues that might arise during the current management of the Oostvaardersplassen ICMO (2006, 2010).<sup>5</sup> It is obvious that animal welfare issues cannot simply be addressed using biological measures, but involve a complex compromise between scientific formality and public perception.

### **Conclusions**

Early definitions of the concept of animal welfare were primarily based on an exclusion of negative attributes. They neglected the fact that during evolution animals have optimised their ability to interact with and adapt to their environment(s). Welfare as a biological function, embracing the continuum between positive and negative welfare, should take into account the dynamics of the individuals' adaptive capacity. Positive welfare implies that the animal has the freedom and capacity to react appropriately (i.e. adaptively) to both positive and potentially harmful (negative) stimuli. Consequently, within the framework of the assessment of the biological aspects of animal welfare, it is of utmost relevance to evaluate whether an animal is able to fulfil the demands of the respective environmental circumstances, given the limits of the animals' capacity to adapt. The application of this dynamic welfare concept - based on the adaptive capacity of an individual - has significant implications for practical welfare assessments: only the change in response towards a given stimulus over time will tell us whether an individual was able to adapt to that stimulus.

Animal welfare issues cannot be addressed without due consideration of the public moral values alongside the more objective analysis of the animals' biological functioning, contributed by animal scientists. Professionals who are expected to advise on animal welfare issues must take this complex interplay into account.

### **Conflict of interest**

Neither of the authors of this paper has a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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<sup>&</sup>lt;sup>4</sup> Koninklijke Nederlandse Maatschappij voor Diergeneeskunde (Royal Netherlands Veterinary Association).

<sup>&</sup>lt;sup>5</sup> International Commission on the Management of the Oostvaardersplassen (ICMO).

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