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Ethology applied to animal ethics☆

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ABSTRACT

According to modern animal welfare legislation, animals should be protected from suffering and lasting harm not for the benefit of us humans as in earlier anthropocentric conceptions, but in their own interest. The driving force behind animal protection is our empathy with animals which triggers feelings of compassion. Empathy with animals most likely is a psychological side-effect of adaptive empathy among humans, and its expression is largely determined by the degree of similarity between animals and us in morphology and behaviour. As a result, compassion with animals is vulnerable to anthropocentric bias, prejudice, and deception, and animal protection based on compassion is likely to be unfair towards animals. Moreover, from an ethological perspective, protecting animals in their own interest represents true altruism which places considerable ethical demand on us. However, there may be hidden selfish intentions that question the altruistic nature of animal protection, while at the same time facilitating its implementation. For example, animal protection could help to avoid unpleasant feelings induced by witnessing cruel actions towards animals. Alternatively, exhibiting a caring personality towards animals could represent human social behaviour that pays off indirectly through building up a caring reputation. It is, therefore, important to distinguish between our intention to protect animals (which may be partly selfish) and true animal protection that needs to be justified biologically by values that apply to the animals. Based on the sentientist nature of animal welfare legislation, the greatest challenges to applied ethologists, and important ones as testified by this special issue, are (i) to determine sentience in animals and (ii) to establish valid and reliable measures of affective states such as suffering and well-being. However, there are promising measures of animal welfare beyond measures of affective states. In particular, biologically meaningful measures of 'integrity of form and function' may provide powerful indicators of animal welfare. The integrity concept originates in biocentric ethics and goes beyond sentientism, as it can also be applied to non-sentient animals and even plants. However, when applied to (potentially) sentient animals, it appears to be consistent with our common sense notion of animal welfare which also respects the animals' 'nature' or 'telos'. Moreover, the integrity concept would relieve scientists from solving the 'hard problem' of animal consciousness first, or from establishing valid measures of demand or aversion that are notoriously difficult to establish. In particular, measures of behavioural integrity could offer an opportunity for applied ethology to strengthen its impact on ethical and legal decision-taking, thereby advancing animal welfare without compromising scientific credibility.

1. Introduction

Animal protection is protective behaviour of humans towards non-human animals (further referred to as

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animals). Besides knowledge of the animals' biology, animal protection is determined by our ethics. Despite the great variety of ethical views on human–animal interactions, current debate is dominated by two competing approaches: animal welfare and animal rights (Regan, 1998). Animal welfare refers to the humane use of animals with the aim to minimize suffering and lasting harm. It is based on utilitarian thinking according to which a greater benefit of an action outweighs a greater amount of animal suffering or harm (Singer, 1975). In contrast, the animal rights view is based on deontological thinking. It holds that using (some) animals is wrong by itself and that, like us, (some) animals should be given absolute rights to protect them from being exploited for human purposes (Regan, 1983, 1998) or – in milder forms – from particular human actions, such as those that induce suffering or lasting harm (Broom, 2003).

Whether we should safeguard the animals' welfare or give them rights is not a question that applied ethologists are usually concerned with, because it is not a biological question. It is a philosophical and eventually political question that philosophers, cultural anthropologists, jurists and politicians are concerned with. However, their conclusions may have profound implications for the research agenda of applied ethologists, because the ethical framework determines the kind of ethological evidence that may inform ethical decision-taking.

Despite differing views on why and how animals should be protected, most welfarists and rightists share a sentientist view according to which sentient animals in particular should be protected (Linzey, 1998), and that they should be protected in their own interest. This view differs from earlier anthropocentric views according to which animals were protected for the benefit of humans, including the preservation of human morality (Rowan and Rollin, 1983). Therefore, both welfarists and rightists depend on biological knowledge about the nature of sentience and its distribution in the animal kingdom, about the extent to which animals are capable of subjective experiences, and about the consequences for the animals' well-being when their ecological and behavioural needs are not met. Note that I will use 'well-being' complementary to 'suffering' throughout this paper. Thus, while suffering refers to 'negative affective states', well-being refers to 'affective states that are not negative' (i.e. neutral or positive).

These are difficult and complex issues to study. Not surprisingly, therefore, animal welfare science has become one of the most comprehensive and complex disciplines in biology (Dawkins, 2006). It involves theories, concepts and methods from evolutionary biology, behavioural ecology, neurobiology, genetics, physiology, clinical veterinary science and psychology, to name but the most obvious ones. Such multidisciplinary science is highly demanding, yet crucial, if our ethical concerns over animals are to be addressed in the animals' own interests.

However, not only *how* animals should be protected, but also *why* we want to do this in the first place, is a biological question. After all, animal protection is human behaviour. In the first part of this paper, I will therefore explore the ethological basis of human preferences and values in relation to animal ethics. This is not meant to advocate 'biologistic' animal ethics, whereby decisions about *what ought to be* are derived from *what is*. Rather, I take an ethological perspective on animal protection with a view to better understanding how our own behavioural biology shapes our attitudes towards animals. Such understanding seems crucial in view of avoiding unjustified anthropocentrism and uncritical anthropomorphism. Moreover, there are ethical views beyond sentientism such as zoocentrism or biocentrism (Rollin, 1992; Verhoog, 2005), and modern animal welfare legislation to a large extent expresses a compromise between these different views. Based on the ethical principles underlying modern animal welfare legislation, I will use the second part of the paper to discuss actual and potential targets and methods of ethological animal welfare research in terms of their significance for ethical and legal decision-taking. Thus, the meaning of the title of this paper is twofold. In order to provide a framework for this special issue on animal suffering and welfare, it addresses both the human ethology behind our attitudes towards animals and the ethological approaches that may best contribute to animal protection.

2. The ethological basis of human attitudes towards animals

Animal protection is human behaviour and as such an almost universal phenomenon, albeit highly variable in its expression throughout human history and between ethnic groups and civilisations (Fraser, 2009). Such universality strongly suggests that our intention to protect animals is at least partly rooted in our own biology, yet little is known for sure about the exact nature of these roots (Broom, 2003).

Most contemporary views on animal protection are sentientist in nature (Linzey, 1998; Badura, 2001). They are based on the assumption that some animals are capable of experiencing feelings of suffering and well-being. Even those scientists who refer to the 'functioning of the organism' or the 'naturalness of the behavioural repertoire' primarily do so for pragmatic reasons. Thus, normal bodily functions and a full expression of the behavioural repertoire are used as proxies for well-being that are, however, easier to assess objectively (Duncan and Fraser, 1997). The common view of animal welfare scientists is, therefore, the very expression of sentientist animal ethics. The animal rights view is, however, no less sentientist, as its proponents commonly use sentience as the relevant criterion for the attribution of animal rights (Regan, 1983; Ryder, 1989).

We could use other criteria to define the target of our ethical concerns. Indeed, it is increasingly common to refer to zoocentric or even biocentric views and to employ ethical criteria that were previously restricted to human ethics, such as 'integrity of form and function' (Rutgers and Heeger, 1999; Verhoog, 2005) or 'dignity of the creature' (Teutsch, 1995). Integrity as an ethical criterion applies to all living organisms, but may be restricted to animals or extended to abstract categories (e.g. species) or even non-living natural objects (e.g. mountains, forests, crystals;

Verhoog, 2005). Dignity is defined as "the state of being worthy of honour or respect" (The Oxford Encyclopedic English Dictionary, 1991), whereby human dignity refers to the 'intrinsic worthiness' of every human person, which is also the basis of all human rights. Until now, Switzerland is the only country to protect the 'dignity of the creature' (Bundesverfassung, 1999). When introduced to the Swiss constitution by public vote in 1992, however, 'dignity of the creature' essentially meant the same as 'integrity of form and function' (as revealed by the French version, where 'Würde der Kreatur' is expressed as 'l'intégrité des organismes vivants'). It was primarily aimed to protect the species-specific characteristics of animals that were perceived to be threatened by the rapid advances in genetic engineering. While the dignity concept appears inadequate for application to animals, partly because 'being human' is a defining property of 'dignity', the concept of animal integrity could represent a useful addition to a sentientist conception of animal protection (Schmidt, 2008).

From a biocentric perspective, harvesting a lettuce for a salad and (humanely) killing a pig for a stew represent similar degrees of ethical offence. Given both the pig and the lettuce are survival machines employed by genes to compete in natural selection (Dawkins, 1976), there is no *a priori* reason why we should deny the lettuce, but not the pig, our ethical concern. Yet this is exactly what we do by using sentience as the relevant criterion in animal ethics. Considering nature as a whole, this is of course an arbitrary decision. It means to discriminate entire taxonomic groups of organisms based on the presence or absence of a specific phenotypic trait (i.e. sentience) or expression of that trait (i.e. well-being). In this respect, 'sentientism' is analogous to 'speciesism', the discrimination of animals that do not belong to the species *Homo sapiens* (Singer, 1975; Linzey, 1998). This analogy is relevant because the arbitrariness of the speciesist nature of animal welfare legislation is a major target of criticism by both utilitarian animal welfarists and deontological animal rightists (Singer, 1975; Regan, 1983, 1998). However, a shift from a sentientist position to a biocentric position could have far reaching implications as discussed in a recent editorial in the journal Nature highlighting how the Swiss 'dignity' law threatens plant biology (Abbott, 2008).

2.1. Empathy and compassion

It is, of course, not entirely arbitrary why the slaughtering of a pig, however humanely, matters more to us than the harvesting of a lettuce, and why we have difficulties in appreciating the 'dignity' of a lettuce. It *feels* so. This is where our own biology kicks in. We feel sorry for the pig because we map the pig's experience of that situation on our own (imagined) experience of a similar situation. 'Feeling sorry for' is everyday language for compassion, a profound (human) emotion prompted by the suffering of others. Compassion commonly leads to an active desire to alleviate another's suffering. Compassion is thought to be facilitated by empathy, "the tendency that most people have to be emotionally affected by witnessing the emotion (e.g. pain) of another person" (Paul, 1998). More empathic persons tend to show greater compassion. Moreover, empathy with people and empathy with animals seem to covary (Paul, 1998). As a matter of fact, most people show a stronger emotional response to the slaughtering of a pig than to the harvesting of a lettuce.

But where does this emotional response come from? One possibility is that it is triggered by our ethical principles, however arbitrary these may be. Because we have learnt that slaughtering a pig is a greater moral offence than harvesting a lettuce (because the pig, but not the lettuce, is sentient), we show a stronger emotional response to the slaughtering of the pig. This could occur through the internalisation of a social norm according to which killing sentient organisms is morally worse than killing non-sentient organisms. There is indeed some evidence that the perception of violations of social norms can induce emotional responses known as moral emotions (Mercadillo et al., 2007). However, ethicists and biologists widely agree that the causal relationship is just the other way round. Thus, instead of ethics affecting our biology, it is our biology that has shaped our ethical views (Singer, 1981; Ridley, 1996). Indeed, there is strong evidence that social norms are enforced by moral emotions (Fessler, 2002).

Most likely, we feel sorry for the pig because we do indeed empathise with the pig (but not with the lettuce). Pigs and many other animals possess characteristics that are able to elicit our empathy. Supported by their look, we tend to interpret the pigs' behavioural responses (postures, vocalisation, etc.) to specific conditions as expressions of their emotional states, hence our empathy. This could explain our tendency to attribute a higher moral status to pigs than to lettuces.

2.2. Empathy with animals: adaptive or artefact?

Although empathy with animals is the driving force behind animal protection, its biological function has received little attention. In fact, it is not obvious at all why humans should empathise *with animals*. However, the answer to this question may be key to our understanding of the biological basis of human values that determine animal ethics. We may thus revert to asking what empathy *in general* might be useful for, and under what circumstances it may have evolved.

The 'empathy-altruism hypothesis' (reviewed by Batson and Shaw, 1991) suggests that empathy motivates altruistic behaviour, and its proponents claim that it explains true altruism. This begs the question as to where empathy came from in the first place. From an evolutionary perspective, the 'empathy-altruism' hypothesis has no explanatory value unless the evolution of empathy is seen in light of the evolution of altruism. Empathy most likely evolved as a mechanism that facilitates kin selection and reciprocal altruism (Broom, 2003). For example, parents who empathise with their children will provide better child care. They will prevent their children from dangers and will care for them when their welfare is at stake. Empathy is elicited by specific signals. For example, a face distorted in pain or a scream may trigger behaviour aimed at removing the cause of these signals. That

'altruistic' behaviour towards close kin and close relations may increase inclusive fitness is well established (Fehr and Fischbacher, 2003). If empathy facilitates such behaviour, it can have adaptive value in this context. There is indeed strong evidence that empathy is biased towards kin and close relations (Kruger, 2001), and that kinship and reciprocal altruism are the best predictors of our intention to help (Kruger, 2003). According to the 'altruism theory', however, empathy with animals must be an artefact resulting from our predispositions to show empathy with humans.

The 'simulation theory' of empathy (Gallese and Goldman, 1998) is a viable alternative to the 'altruism theory'. Based on the discovery of 'mirror neurons' in macaques (di Pellegrino et al., 1992) and a similar neural system in humans (Iacoboni et al., 1999), the simulation theory views empathy as a form of 'mind reading', allowing us to assess the mental states of others to better predict their future actions (de Vignemont and Singer, 2006). In theory, therefore, empathy with animals might be adaptive by allowing us to better predict their intentions. This raises the intriguing possibility that our feelings of empathy with animals might indeed reflect their true emotional states. This would open up exciting new ways of assessing animal welfare, and provide a convincing biological rationale for the assessment of emotional states in animals using the 'Qualitative Behaviour Assessment' methodology proposed by Wemelsfelder (2007). Thus, on-farm assessments of animal welfare could simply be carried out by careful introspection.

However, our tendency to empathise with animals increases with increasing similarity in their look and behaviour. Indeed, the recognition of ourselves in others (DU-Evidenz) is an important determinant of our compassion for animals (Gärtner, 1980). This explains why our compassion for primates is stronger than for other mammals (as currently evidenced by several initiatives to ban research on non-human primates), and still stronger than for birds, reptiles or fish. With respect to the simulation theory, this would mean that the significance of knowing about an animal's state of mind decreases with decreasing similarity with us. If empathy with animals had evolved in view of true mind-reading, however, one would not necessarily predict such a similarity-based relationship. Not similarity in the looks and behaviour, but significance for our survival (e.g. as a predator or prey) would be expected to correlate with the expression of empathy. Although the simulation theory may explain empathy with humans, there is no evidence that empathy with animals is based on adaptive mind-reading.

The altruism and simulation theories of empathy are not necessarily mutually exclusive. Regardless of which hypothesis applies to empathy with *humans*, however, there is no evidence that empathy *with animals* has any adaptive significance. Empathy with animals most likely is a psychological side-effect of empathy with humans and thus a biological artefact. Presumably, it is triggered by animal signals that sufficiently closely resemble those human signals that trigger adaptive empathy among humans. However, if empathy with animals is a side-effect of empathy with humans based on human-like animal signals, subjective assessment methods of animal well-being (e.g. Wemelsfelder, 2007) will be highly vulnerable to anthropomorphism.

2.3. Animal protection: altruistic or selfish?

In contrast to earlier anthropocentric approaches, where animals were protected to preserve human morality, modern animal ethics implies that animals be protected in their own interest. This places considerable ethical demand on us. It means to dismiss potential benefits from certain kinds of animal use for the sake of preserving the animals' own interests. From an ethological perspective, such behaviour would qualify as truly altruistic (Ridley, 1996). According to evolutionary theory, however, true altruism (in terms of inclusive Darwinian fitness) exists but as an artefact and is counteracted by natural selection.

One could argue that altruistic animal protection is based on cultural rather than natural selection. Supported by our natural tendency to empathise with (some) animals, compassion with animals could have become a particularly successful meme (Dawkins, 1976) in the memepool of views on human–animal interactions. The costs of adhering to altruistic animal ethics may generally be too low for the average human being to have significant fitness consequences. This is supported by the fact that the degree of concern over animal welfare tends to be positively correlated with human welfare. However, for an idea that is at odds with fundamental principles of natural selection to be so successful, it is likely to have some hidden benefits. Thus, our intention to protect animals from suffering may not necessarily reflect truly altruistic behaviour.

There may indeed be selfish intentions behind animal protection, one of which emerges from the biology of empathy as discussed above. If animal signals are able to trigger feelings of empathy, then witnessing suffering-like signals in animals can make us truly feel bad. Protecting animals from conditions that elicit such signals could represent a way to avoid such unpleasant feelings. Selfish intentions become even more apparent when animal protection is regarded as a form of human *social* behaviour. What at first sight looks like altruistic behaviour (e.g. donating money, helping others) often turns out to be a form of indirect reciprocity – behaviour that benefits one's reputation within one's social environment (Nowak, 2006). Perhaps we do indeed pay lip service when claiming to protect animals in their own interest, while what we are actually doing (however unconsciously) may in fact be rather selfish: do good and speak about it. This would also explain why the 'ethics of care and compassion' (Noddings, 1984) is so appealing to many people. According to this approach, the highest level of ethical conduct to achieve is "to develop and demonstrate compassion for others". Such ethics will also benefit animals, but only indirectly, as a side-effect of demonstrating (to other humans) compassion for animals e.g. by good stockmanship. However, the ethics of care and compassion is plain anthropocentric animal ethics which is considered morally 'inferior' to modern animal ethics as specified above (Rowan and

Rollin, 1983). Moreover, because compassion is affected by empathy, an ethical framework based on compassion shows its limitations most clearly when our empathy becomes excessive (e.g. in the face of zoo-cuties such as polar bear cubs) or when it breaks down (e.g. in the case of 'pest animals'). Indeed, there is a striking contrast between the cruelty of 'pest control' (Littin and Mellor, 2005) and the almost human-like moral status attributed to animals that are close kin (great apes), look similar or otherwise attractive to us (e.g. bears) or are our closest companions in life (e.g. dogs, cats, horses). Importantly, this clash of attitudes is largely independent of our 'official' criterion for the protection of animals – the degree to which they may be capable of suffering.

2.4. Deception and prejudice

If you were ever moved to tears in a movie theatre, you have experienced how easily compassion can be deceived. Although the signals that move us to tears in a movie theatre may have exactly this function in real life, the same signals also function out of context (e.g. in a movie). Without implying that animals actively parasitise our psychological predispositions to empathise with them, we cannot exclude the possibility that animals may sometimes unintentionally behave *as if* they were in pain or suffering without actually being in pain or suffering (and, of course, vice versa). Moreover, unfair prejudice is not restricted to the lay public in the face of 'zoo-cuties' and 'pest animals'. Even experts may be taken in by prejudice. For example, in a recent survey among veterinary students, more than 50% of the students considered castration with a rubber ring to be a humane method of castration for cattle and sheep, while less than 10% considered the same method humane for dogs or cats (Levine et al., 2005). There is no real evidence that this procedure is less painful for sheep than for dogs. The different ratings merely reflect the students' prejudice about the different animals' abilities to experience pain and the animals' relative moral status, possibly due to different degrees of 'Du-Evidenz'.

In conclusion, our compassion for animals and thus our tendency to protect them is likely to be affected by our tendency to empathise with them. Empathy with animals most likely is a psychological side-effect that is based on the animals' similarity with us humans (DU-Evidenz) and specific signals that sufficiently closely resemble those human signals that trigger adaptive empathy among humans. As a result, compassion with animals is highly vulnerable to deception and prejudice. Therefore, compassion with animals does not provide a reliable basis for animal protection, at least not against the ideal of modern animal ethics according to which animals should be protected in their own interest. Animal protection based on compassion with animals is likely to be unfair to (many) animals. It is, therefore, important to distinguish between our intention to protect animals (which may be partly selfish) and true animal protection. Animal protection is ethically justified by our own human values. What animals need for their protection, however, needs to be justified biologically by values that apply to the animals. Only by acknowledging this distinction will we arrive at an ethical and legal framework that satisfies our ethical claims as well as doing justice to the animals.

3. Ethical principles in animal welfare legislation

Modern animal welfare legislation is based on hybrid animal ethics, a dualistic mixture of deontological and utilitarian ethics involving anthropocentric, sentientist and biocentric principles. By default, all human beings have higher moral standing than all other animals (anthropocentrism). Furthermore, all sentient animals have higher moral standing than all non-sentient animals, and the extent of suffering imposed by an action determines its ethical severity (sentientism). In contrast to humans, however, animals are not given absolute rights of freedom from suffering since 'higher' ends may justify virtually any degree of suffering (utilitarianism). Finally, no animal shall be harmed or killed without justification, even if the harm or killing does not cause any suffering (biocentrism).

The fundamental ethical divide between humans and animals cannot be justified biologically. It is entirely arbitrary and often referred to as *speciesism* (Ryder, 1989). That animal welfare legislation is based on such arbitrary discrimination of other beings is disturbing to purist ethicists. Attempts have thus been made to replace speciesist ethics by more consistent ethical principles. From the dualistic nature of animal welfare legislation based on deontological and utilitarian views, two extreme forms of pure ethics have been put forward: pure deontological ethics in the form of animal rights (Regan, 1983) and pure utilitarianism (Singer, 1975). Animal rightists attempt to overcome speciesism by extending absolute rights to (some) animals, while utilitarians pursue the same goal by extending utilitarianism to humans.

Animal rights could have far reaching implications for society. In its most extreme form, this may go as far as a total ban of animal research (at least on vertebrates) and animal farming, and even questions the right to possess companion animals. This is considered a fundamentalist position that lacks public support (Browne, 2006), except in the case of higher mammals such as the great apes (Scharmann, 2000) or when formulated in terms of weaker rights (Warren, 2000). Regardless of its lack of majority appeal, however, animal rights fail to solve the ethical dilemma they are intended to address. Extending moral rights e.g. to all sentient animals as proposed by many animal rightists (Regan, 1983) still involves the arbitrary discrimination of non-sentient creatures, referred to above as *sentientism*. Even including all animals would fail to overcome such arbitrary discrimination (sometimes referred to as *kingdomism*). Such criticism may appear sophistical. From a biocentric perspective, however, the situation looks different. As discussed above, the 'dignity' of plants is already an issue, even if only in Switzerland (Abbott, 2008). Thus, attempts to overcome arbitrary discrimination in the form of speciesism by extending human rights to (some) animals would only shift borders along which arbitrary discrimination occurs (although this would undoubtedly benefit large numbers of animals).

In contrast, pure utilitarianism might overcome such arbitrary discrimination all together by applying a single

ethical principle to all human actions, regardless of whether those affected were humans or animals (or, in fact, any other living organism). Pure utilitarianism is considered equally extreme and fundamentalist by today's standards, mostly because of its challenge to human rights and the moral equality of human beings. More importantly, however, the ethical costs and benefits of human actions, which form the basis of ethical decisions in utilitarianism, are impossible to quantify objectively. Without an objective yardstick, however, and because utilitarianism accepts an unjust distribution of benefits and burdens among individuals (Rawls, 1957), utilitarianism is likely to induce unfairness of a different kind.

Because any form of pure (animal) ethics fails to address the complexity of animal protection, less radical, hybrid views are likely to persist, even if these appear inconsistent to a purist ethicist. It has been argued that the utilitarian principle of 'minimizing animal suffering' may be the least denominator to which a large majority might agree (Mayr, 2007). It is centred on the main issue of our ethical concerns over animals (the possibility of their suffering) and is likely to matter to the animals themselves (as shown by their tendency to avoid conditions that are likely to induce suffering). At the same time, it allows for sufficient flexibility in the way we use and interact with animals. However, as further discussed below, focusing on subjective well-being (or absence of suffering) may be too narrow an approach both for ethical and scientific reasons. It has thus been argued that the biocentric criterion of integrity of form and function may provide a useful addition to sentientist animal welfarism (Schmidt, 2008).

4. Ethological approaches to the assessment of animal welfare

Because of the sentientist conception of animal welfare legislation and the utilitarian approach to ethical decision-taking, ethology applied to animal ethics has two main targets, namely (i) to determine sentience in animals and (ii) to assess the degree of animal suffering imposed by human actions. Only sentient animals can be targets of sentientist animal ethics, and the extent of suffering (or well-being) is the animals' currency in the utilitarian cost-benefit analysis.

4.1. Animal sentience

Sentience refers to the ability of animals for affective states, including feelings of suffering and well-being. However, affective states are subjective and cannot be assessed objectively (i.e. from a third person perspective) by scientific methods (Nagel, 1974). As a result, the line between sentient and non-sentient animals is drawn at different taxonomic levels by different scientists using different criteria. Given that subjective experiences are scientifically inaccessible, however, any biological criterion of animal sentience remains somewhat dubious. This may explain why animal welfare scientists generally avoid drawing that line. For example, in a recent special issue of *Applied Animal Behaviour Science* (2006, vol. 100, issues 1–2) on 'Sentience in Animals', not a single author made an attempt to draw that line. In order to distinguish between sentient and non-sentient animals, we need to know exactly what it needs (both in terms of 'hardware' and 'software') for sentience to emerge in animals, and how it is expressed in physiology and behaviour. As long as we do not know that, the scientific underpinnings of sentientist animal ethics remain shaky. All we can provide is the benefit of the doubt based on an argument by analogy (Sambraus, 1995).

Despite having access to verbal reports, even medical doctors diagnosing pain or anxiety in human patients may need an argument by analogy. Not all patients are capable of verbal reporting and verbal reports may include lies. This is nicely illustrated by the difficulties in diagnosing pain from whiplash and the ensuing fights over health insurance money (Ferrari, 2005). Thus, the difficulties in diagnosing pain or anxiety in animals vs. humans are not different in kind, but different in degree. How different they are depends on differences between the animals and us (i) in nervous system architecture and function, (ii) in the significance of external stimuli, and (iii) in the responses to these stimuli, i.e. the three building blocks of the argument by analogy (Sambraus, 1995).

Recent studies in fish have shown how powerful a case can be made for animal sentience on the basis of an argument by analogy. Thus, Dawkins (2008) stated: "If you believed that it was wrong to inflict pain on an organism and also thought that fish did not feel pain, you might feel it was morally acceptable to cut up living fish or fish with hooks. But if you then came across some of the newer evidence that suggested that fish feel pain (Chandroo et al., 2004; Sneddon et al., 2003), you might begin to reconsider your behaviour". Recently, similar research in crustaceans has started to make a case for sentience in some invertebrates (Elwood et al., 2009). The kind of evidence that is available for making a case for sentience in animals may become increasingly refined with scientific and technological advances. However, some form of argument by analogy will remain the conceptual tool that is needed to integrate such evidence to make a plausible case for sentience – or to put it in Galileo Galilei's words, to "make measurable what is not so".

4.2. Suffering and well-being

Although the term suffering covers a wide range of different emotional states such as pain, fear, thirst, hunger, boredom etc., we use a single term, because what seems important is that they are all unpleasant enough for an animal to want to get out of them (Dawkins, 2008). Dawkins concludes that this "behavioural way of recognizing suffering. . .provides us with a way of recognizing animal suffering in an objective way". In line with Rolls (2005) she defines emotions as instrumental reinforcers, as states elicited by rewards and punishers. Thus, suffering can be caused either by the presence of punishers (e.g. predators) or by the absence of reinforcers (i.e. deprivation; Dawkins, 2008).

The problem with instrumental reinforcers as indicators of animal emotions is that operant conditioning also works in invertebrates such as Drosophila (e.g. Brembs and

Heisenberg, 2000) and Aplysia (e.g. Cook and Carew, 1986), animals that most scientists would deny the capacity to *feel* pain. Anticipating such criticism, Dawkins (2008) further stated that "emotional states, as defined by what animals find positively or negatively reinforcing *may* be accompanied by subjective feelings of pleasure or suffering but not necessarily" (note that Dawkins here confused 'negative reinforcement' with 'punishment'). Once again, we find ourselves trapped in the third person perspective. Thus, instrumental reinforcers may be useful tools for assessing suffering and well-being, but only in those animals for which we have made a convincing case that they *are* sentient.

Another problem with instrumental reinforcers is that they are rather indirect measures of suffering and well-being. Thus, we need to assess how much animals will work to gain access to or avoid particular conditions, which we then interpret in terms of how well animals will be feeling when deprived of or exposed to these conditions. Studies in mink indicate that measures of demand can be good indicators of acute stress when a previously available resource suddenly becomes unavailable (Mason et al., 2001). However, they may be unreliable indicators of suffering from deprivation, i.e. suffering from the absence of a resource that has never been experienced before, which is what we are really interested in.

Finally, there are serious conceptual and technical difficulties in obtaining valid measures of demand or aversion (Houston, 1997; Kirkden et al., 2003; Kirkden and Pajor, 2006; see also Asher et al., 2009). These difficulties may explain why so far this approach has had rather little impact on the development of animal housing systems (but see Manteuffel et al., 2009 for promising ways to implement cognitive enrichment by use of instrumental reinforcers).

Recently, a somewhat more direct way of assessing animal emotions has been pioneered by Mendl and colleagues (Harding et al., 2004; Mendl and Paul, 2004; Paul et al., 2005; see also Mendl et al., 2009; Brilot et al., 2009). This approach accepts that feelings cannot be measured directly, but uses cognitive measures (e.g. cognitive bias) that are known from human cognitive science to correlate with emotional valence (Paul et al., 2005). Measures of cognitive bias are particularly promising for two reasons. First, they promise to measure what we aim to measure, namely the animals' state of mood under the conditions under which they live. Second, such measures of mood state might be particularly suitable for in-situ application on farms, in laboratories, or in zoos. Thus, cognitive measures of emotional state are an exciting addition to the tools of applied ethology for determining animal sentience and assessing animal well-being and suffering. Unfortunately, however, these measures currently depend on complex learning protocols and extensive training sessions. Besides being very time consuming, the training might also affect the animals in ways that interfere with the measurement of their emotional states. Researchers have thus started the search for cognitive measures of emotional state that are based on spontaneous behavioural responses, albeit as yet with limited success (see Brilot et al., 2009).

4.3. Integrity of form and function

According to Dawkins (2006), animal welfare depends on two aspects, namely (i) whether the animals are healthy and (ii) whether they have what they want. The second aspect refers to measures of demand and other measures of affective state as discussed above, while the first aspect refers to physical and mental health. In principle, impaired physical or mental health might thus be considered as a welfare problem regardless of whether it is associated with impaired well-being. However, the underlying assumption has always been that well-being is a function of both aspects, and at least some authors explicitly stated that all that really matters is the animals' subjective experience (Duncan, 1993). According to them, health primarily addresses long-term consequences for well-being which may conflict with short-term choices in animals (e.g. in the case of obesity in dogs fed ad libitum).

The problem with such a narrow conception of animal welfare in terms of subjective experience is that it is difficult to say exactly what we mean by well-being. Is it the absence of suffering, a fair balance between states of suffering and pleasure, or constant pleasure? Most people would probably agree that there is nothing wrong with the ethical principle of minimizing animal suffering, but what about maximizing animal pleasure (see also Balcombe, 2009)? In fact, we would have the means to induce feelings of pleasure by administering psychoactive drugs or by electrical stimulation of specific brain areas. While this might well result in happier animals, it is not what our common sense notion of animal welfare is about. Implicitly, our notion of animal welfare has to do with the integrity of the animals' 'nature' or 'telos' (Rollin, 1992). In ethical terms, such a notion goes beyond sentientism and relates to biocentric views. Some ethicists translate 'telos' into 'dignity of the creature'; from a biological perspective, however, and because of the difficulties with the term dignity (as discussed above), I prefer to translate it into 'integrity of form and function' (further referred to as 'integrity').

With the advent of genetic engineering, physical and mental integrity have become highly relevant ethical issues (Schmidt, 2008). The assessment of the animals' integrity goes beyond applied ethology. However, applied ethology has the means to investigate how integrity can be addressed in ways that are consistent with both the animals' behavioural biology and with their well-being. Moreover, integrity may to some extent relieve animal welfare scientists from the burden 'to make measureable what is not so' (i.e. subjective experiences). This is illustrated by the controversy surrounding the question as to whether stereotypies are a good or bad indicator of poor welfare. Thus, decades of research failed to make a convincing case for suffering being associated with their performance (Mason and Latham, 2004), while it appears relatively simple to study whether stereotypies reflect neurological dysfunction (Garner, 2006). From a biocentric perspective, neurological dysfunction is readily accepted as a measure of poor welfare, regardless of whether or not it is associated with suffering. Neurological dysfunction also violates Dawkins' first criterion of animal welfare ('are

the animals healthy?'), but only if we are ready to go beyond a sentientist conception of animal welfare.

Like suffering, integrity is a normative rather than a biological term, and its precise biological meaning may be elusive. The same is true for health, and in many ways, health and integrity may be considered as the same thing. However, instead of using impaired integrity simply as a proxy of impaired well-being (i.e. suffering), it may be used as an indicator of poor welfare in its own right. For example, if defined by its cause rather than its consequences as "a maladaptive phenotypic expression caused by dysfunction of one or several parts of the body" as proposed for pathology (Würbel, 2006), impaired integrity may become a useful concept in the assessment of animal welfare, regardless of its implications for subjective well-being. Moreover, the integrity concept provides measures of animal welfare that are consistent with our common sense notion of 'animal welfare', without the need to solve the 'hard problem' of animal consciousness. This is further illustrated by the use of behavioural integrity in the development and welfare assessment of animal housing systems.

4.4. Behavioural integrity

Integrity of behaviour refers to both the naturalness of the animals' behavioural repertoire and the normality of its expression. Much of applied ethology in the 1970s and early 1980s was implicitly based on such a conception of behavioural integrity, especially research aimed at developing welfare-friendly housing systems for farm animals. Thus, several groups conducted detailed ethological studies on farm animals living under natural or near-to-natural conditions. Their aim was to identify key stimuli that facilitate the expression of the animals' natural behavioural repertoire and the performance of normal behaviour (e.g. pigs: Stolba and Wood-Gush, 1984; laying hens: Fölsch et al., 1983; rabbits: Stauffacher, 1992). The assumption underlying these studies was that allowing animals to perform their natural behaviour by incorporating these key stimuli (or adequate substitutes thereof, Stauffacher, 1994) would guarantee their welfare. Implicitly, therefore, 'behavioural integrity' as defined above was used as a measure of animal welfare. Moreover, most guidelines for animal housing (e.g. the revised Appendix A of ETS No. 123) are implicitly based on behavioural integrity when advocating environmental enrichment "to allow expression of a wide range of normal behaviour".

More recently, however, 'the naturalness of the behavioural repertoire' has been heavily criticised as a poor measure of animal welfare by several applied ethologists (Duncan and Fraser, 1997; Dawkins, 2008). Dawkins (2008) for instance argued that some behaviours such as being chased by a predator may well be natural but unlikely to promote good welfare. Indeed, being chased by a predator is unlikely to be positively reinforcing, in contrast e.g. to the opportunity to scratch and dust bathe in hens. However, not 'being chased by the predator' is the natural behaviour in question, but 'running away in the face of a predator', in which case Dawkins' criticism evaporates. The difference to scratching and dust bathing in hens is that these are largely *internally* motivated behaviours, while running away in the face of a predator is entirely *externally* motivated. However, even if predators are kept away from captive animals, the ability to perform normal anti-predator behaviour may still be crucial for their welfare. For example, although laboratory mice never face real predators in the laboratory, the laboratory environment is full of stimuli (e.g. manipulations of care takers, noise, light etc. as well as odour cues of e.g. rats or cats) that can elicit anti-predator responses. Sheltered areas in the cage will provide for the performance of normal anti-predator behaviour and thereby contribute to both the animals' behavioural integrity and their subjective well-being. Thus, if restricted to (i) behaviours that are strongly internally motivated and (ii) behavioural responses for which eliciting stimuli are likely to be present in the environment in which the animals are being kept, behavioural integrity will be fully consistent with Dawkins' second criterion of animal welfare (i.e. "do the animals have what they want"). However, because it may be impossible to determine the proximate factors for all behaviours of the animals' behavioural repertoire, and because of the difficulties of establishing valid measures of demand and aversion, behavioural integrity may be a useful measure of animal welfare to give the animals an ethologically informed benefit of the doubt. Applied ethologists are equipped to work out ways of using measures of behavioural integrity that are ethologically justified and valuable for ethical decision-taking.

5. Conclusions

Animal protection is based on human values that may be affected by bias, prejudice and deception due to our own human biology. What animals need for their protection, therefore, needs to be justified biologically by values that apply to the animals. Because we are part of the animal kingdom ourselves, and because no sharp boundaries exist between us and them, there may be no simple ethical principle that satisfies both our ethical concerns and the interests of the animals. As a result, any purist ethical framework (such as pure deontological or utilitarian ethics) may be doomed to fail in the face of the complexities of animal protection. Similarly, any narrowly defined scientific notion of animal welfare (e.g. by restricting welfare to subjective experience) will fail to do justice to these complexities.

Importantly, the targets of animal protection have to be agreed upon by society as a whole. This includes two questions, namely (i) *who* is to be protected (i.e. which animals?) and (ii) from *what* (death? dysfunction? suffering?), both of which need to be answered separately. For example, if subjective experience were all that mattered, it would seem logical to protect all sentient animals. However, we might still agree on a smaller subset (e.g. all vertebrates), even if this involves arbitrary discrimination of some other subset. As discussed above, there may be no way around some form of arbitrary discrimination. This becomes even more apparent when we extend our notion of welfare from mere well-being to integrity of form and function. Integrity potentially relates to all living organisms (including plants and protozoans). It is therefore factually impossible to

protect the animals' integrity without discriminating a large portion of all living organisms. Importantly, depending on these decisions, the research agenda of applied ethologists may look quite differently.

Determining animals' ability for (conscious) subjective experience (i.e. sentience or consciousness) and establishing valid and reliable measures of suffering and well-being will remain the greatest challenges to applied ethology, and important ones as testified by this special issue. However, applied ethologists should not ignore the many other ways in which ethology may be effectively (and sometimes even more effectively) applied to the broad and developing field of animal ethics. In particular, biologically meaningful behavioural and physiological measures of integrity of form and function may provide powerful indicators of animal welfare, whereby welfare refers to more than well-being, which is also consistent with our common sense notion of animal welfare. Importantly, this may relieve scientists from solving the 'hard problem' of consciousness and may thus provide an opportunity for applied ethology to strengthen its impact on ethical and legal decisions, thereby advancing animal welfare without compromising scientific credibility.

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