

Breeding for pleasure: the value of pleasure and pain in evolution and animal welfare

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Abstract

Farming and laboratory industries face questions about whether to breed animals with altered capacities for pleasure and pain. This paper addresses this issue from different approaches to animal welfare based on experiences, fitness and naturalness. This can illuminate both the breeding-related issues and the different approaches themselves. These differences have practical implications for decisions about animal breeding. All three approaches will agree that pleasure that is adaptive in natural environments has positive value and that maladaptive pain has negative value. However, where animals' environments will not be natural, experiences-based approaches may support breeding animals that experience more pleasure and less pain or insentient animals; whereas, in some cases, fitness-based and naturalness-based approaches might favour the breeding of animals that experience more pain and less pleasure.

Keywords: animal welfare, breeding, extrinsic value, fitness, pleasure, signatory value

Introduction

Recent years have seen an increased recognition that decisions based on animal welfare science involve ethical, as well as scientific, considerations (Tannenbaum 1991; Sandøe & Simonsen 1992; Fraser 1995; Sandøe *et al* 2003; Lund *et al* 2006). Consequently, both philosophico-ethical discussions and scientific investigations can help to clarify the discipline's ethical positions, and to identify practical solutions to animal welfare challenges. Animal welfare science and policy-making can involve many different approaches to the question of what has value for animals. Different approaches often agree about practical issues, but at other times can disagree strongly. Understanding where and why approaches agree and disagree will help to understand the approaches themselves, as well as progress dialogue and individual decision-making.

This paper addresses the practical challenge of whether animals should be bred to have altered predispositions to feeling pleasure and pain. Approaches to animal welfare based on fitness, experiences and naturalness generate different answers to these questions. This investigation provides insights into both animal welfare ethics and the animal welfare implications of breeding.

Breeding for pleasure

Animal welfare approaches may be usefully applied to improve animals' lives through directing breeding strategies (Sandøe *et al* 1996; Jones & Hocking 1999; Kanis *et al* 2005; Olsson *et al* 2005). Some analyses can help to avoid harmful breeding regimes (eg Rauw *et al* 1998).

Others can direct breeding towards improving health (CAWC 2008; UFAW 2009).

An alternative possible application of animal welfare approaches is to breed animals so as to alter their affective systems. There is increasing research into the genetics of affect (Wilson & Mogil 2001; LaCroix-Fralish & Mogil 2009). It may soon be possible to strategically breed animals to have higher or lower capacities for pleasure and/or pain, relative to their natural, wild types.

Many pain traits appear heritable in mice (Mogil 1999; Mogil *et al* 1999a,b, 2000; Shir *et al* 2001) and humans (Norbury *et al* 2007; Nielsen *et al* 2008; Fillingim *et al* 2009) and it has long been possible to breed mouse strains with altered responses to potentially painful stimuli (Belknap *et al* 1983; Panocka *et al* 1986). Indeed, animals might be bred that cannot experience pain. Gene-knockout mice have been created as a model for congenital insensitivity to pain syndromes (Smeyne *et al* 1994; Indo *et al* 1996; Mogil *et al* 2000), and animals might be bred to have damaged or absent cingulate gyri, which might reduce their capacity for pain (Hassenbusch *et al* 1990; Wilkinson *et al* 1999).

There is less known about the genetics of pleasure, but there is evidence that breeding can alter an animal's capacity for pleasure. One study reported that 44–52% of variance in happiness in humans is associated with genetic variation (Lykken & Tellegen 1996). Mice of different strains similarly appear to show different levels of chirping, playfulness, and speed of learning tasks to receive pleasurable tickling (Panksepp & Burgdorf 2000). Indeed,

it may be that some companion animals have already been selected to be predisposed to experiencing pleasure (Spinka personal communication, 2009). Furthermore, breeding for altered capacities for pleasure and pain may affect one another (Breslin *et al* 1992; Feldman Barrett & Russell 1998; Spruijt *et al* 2001; Verhagen & Engelen 2006; Yeates & Main 2008), so that breeding for altered pain sensation may alter animals' capacities for pleasure. Insofar as both are part of a single affective system, breeding animals to be insentient would decrease their capacity to experience both pleasure and pain.

Approaches to animal welfare

The first question is *which* animal welfare approaches should be applied to this issue. There are many different approaches to animal welfare (DeGrazia 1998; Fraser 1998; Sandøe 1999; Appleby & Sandøe 2002; McMillan 2003; Wojciechowska & Hewson 2005; Nordenfelt 2006; Yeates & Main 2009), and each provides different answers.

Fraser *et al* (1997) categorised animal welfare approaches by what they consider to have intrinsic value (for discussions of the concept of intrinsic value see Korsgaard 1983; O'Neill 1992; Rabinowicz & Rønnow-Rasmussen 1999; Heeger & Brom 2001). Some approaches intrinsically value animals' experiences (eg Dawkins 1988; Duncan 1993). Other approaches value fitness or function (eg Broom 1988; Broom & Johnson 1993). A third class of approaches value naturalness (eg Bracke & Hopster 2006).

From these positions, some commentators have called for breeding to increase fitness, especially in terms of health (McGreevy & Nicholas 1999; Lawrence *et al* 2004; MacArthur Clark *et al* 2006). Others have suggested breeding animals to maximise quality of life in terms of pleasure and pain (Sandøe *et al* 1999; McGreevy 2007). Others have promoted naturalness in breeding (FAWC 1998a,b; Nauta *et al* 2009).

In keeping with the themes of this conference, this paper considers experiences in terms of pleasure and pain. Within experiences-based approaches to welfare, pleasure has positive intrinsic value and pain has negative intrinsic value. This paper similarly defines fitness as an evolutionary concept, described in terms of survival or reproduction. On this view, maladaptive states that decrease an animal's evolutionary fitness represent welfare compromises. Likewise, this paper takes the naturalness of an animal to mean how closely it resembles the form that evolved prior to human intervention, and defines the naturalness of an animal's environment as how closely the environment matches (or mismatches) the environment in which the species evolved.

Often, the existence of different approaches is unproblematic, because they agree on important matters, such as system disease and animal abuse. However, differences between the positions can lead to disagreements between people who share the common goal of improving animal welfare. Some commentators have addressed this problem by suggesting pluralistic approaches that combine different elements (eg Dawkins 2003, 2005), such as whether an

animal is fit and happy (Webster 2005). However, combining multiple approaches can make animal welfare assessments more complicated (Mason & Mendl 1993) and disagreements between the different approaches that are included can become internal tensions within the approach.

Investigating cases where different approaches to animal welfare disagree is useful not only to answer the practical questions but also to illuminate the approaches themselves. This can also help individuals to decide their own approach to animal welfare. The value of pleasure and pain is one area in which approaches do disagree.

The value of pleasure and pain

While pleasure and pain have intrinsic value in experiences-based approaches, naturalness-based and fitness-based approaches do not value pleasure and pain in the same way. Naturalness-based approaches value pleasure, pain and affective systems insofar as they are natural. Natural pain therefore has positive value. Recent years have seen the description of sophisticated accounts based on naturalness, which does allow other axiological criteria. For example, Bracke and Hopster (2006) have tried to limit naturalness-based approaches to valuing 'positive' natural states. However, there is nothing in the concept of naturalness to suggest such a restriction of the term. Purely naturalness-based approaches value natural animals, natural environments, natural experiences and natural capacities for pain and pleasure.

Concerning fitness-based approaches, the situation is more complicated. Pleasure and pain do not have intrinsic value in evolutionary fitness-based approaches. There is no reason to expect that the fittest animals are those that have the highest possible capacity for pleasure and least possible capacity for pain. The capacities for pleasure and pain that a species evolves are dependent on what capacities most suit the environment in which it has evolved.

Indeed, animals could theoretically be fit without experiencing any pleasure or pain at all (Morgan 1984; Searle 1984; Hinde 1985; Harrison 1989; Boden 1990; Hauser 1993; Berridge 1996; Dawkins 1998, 2001; Berridge & Winkielman 2003; Winkielman & Berridge 2004; Allen and Beckoff 2007). The autonomic, behavioural and motivational responses that pleasure and pain generate could be stimulated without any experiences (Meadows & Kaplan 1994; Berridge 1996, 2003; Lane *et al* 1997; Dawkins 2000; Gross *et al* 2000; Kelley *et al* 2005). Evolution could therefore have created insentient 'hedonic zombies' that behave like animals that experience pleasure and pain but who do not experience them as pleasant or painful feelings. NB These hedonic zombies are therefore more like the unconscious zombies imagined in philosophy of mind thought experiments (Moody 1994; Chalmers 1996) than the unmotivated zombies of D'Eath *et al* (2010).

In fact, there are reported cases of humans being born with complete insensitivity to pain (Dearborn 1932), while still being able to experience other sensations (Thrush 1973) and perform other functions (Jestico *et al* 1985; Oertel & Löttsch 2008; Hornemann *et al* 2009; Surui *et al* 2009). Mouse pain gene knockouts often survive and develop relatively well

(Mogil *et al* 2000). Indeed, the debates as to whether evolutionarily successful animals, such as fish and invertebrates, can feel pain (eg Cabanac 1979; Sherwin 2001; Seth *et al* 2005) suggest that we consider such animals able to function with or without the ability to feel pleasure or pain.

Fitness-based and experiences-based perspectives therefore disagree philosophically about whether pleasure and pain have intrinsic value. However, there are other ways in which fitness-based approaches may value pleasure and pain that might allow them to agree practically. Pleasure and pain have evolved (Popper 1978; Panksepp 1994; Lindahl 1997), so it seems likely that pleasure and pain do have some evolutionary value. If this is not intrinsic value, then it must be extrinsic value (Smith 1948; Lundberg 1985; Bradley 1998).

There are three types of extrinsic value useful for our discussion. 'Contributory value' is the value something has by being a component of something that has value (Lewis 1955). 'Instrumental value' is the value that something has because it (may) cause another state which has value (see Frankena 1963). 'Signatory value' is the value a state has because it signifies the occurrence of another state that has value (see Feldman 1986). Things with these values are not therefore intrinsically valuable, but relate to things that do have intrinsic value.

To analogise with aesthetic value, imagine that a piece of music has intrinsic aesthetic value. Each note will have contributory value because it contributes to the whole (even though listening to a single note is not aesthetically enjoyable). The training of a musician has instrumental aesthetic value because it allows her to play beautiful music. The applause of the audience has signatory value because it signifies that the music has aesthetic value. Similarly, if animal-based states are argued to have intrinsic value, then inputs such as its environment have instrumental value and outcomes such as productivity or a radiographic image of a bone fracture have signatory value.

Pleasure and pain might be thought of as having contributory value as part of an animal's overall fitness. A well-functioning affective system is part of its overall fitness. This contributory value is a relatively insignificant value, since an animal's affective system is in itself only a minor (and non-vital) contributor to an animal's fitness, especially compared to, say, its heart or its motivational system.

More significant is the instrumental value of pleasure and pain. Pleasure and pain can *lead* to greater fitness, and this is probably why they evolved (Lindahl 1997; Dawkins 1990, 2000, 2001; Broom 1998, 2007; Baars 2002). Notably, they can act as 'rewards' that motivate behaviours that increase fitness (Dawkins 1990; van Ree *et al* 1999; Zald & Depue 2001; Berridge & Robinson 2003; Burgdorf & Panksepp 2006; Wechsler & Lea 2007). As examples, pleasure and pain may cause consummatory, evasive or protective behaviours (Mogil *et al* 2000); modulate learning through conditioning and reinforcement (Cabanac 1971, 1979; Panksepp 1994; Dawkins 2000); direct decision-making (Damasio 1994); alter perception (Berridge 1996); modify cognition (Lerner & Keltner 2000; Désiré *et al*

2002; Harding *et al* 2004; Burman *et al* 2008) and increase fitness through behaviours such as play (Fraser & Duncan 1998; Spinka *et al* 2001). Pleasure may increase animals' health (Pressman & Cohen 2005) and ability to cope with challenge and stress (Lyubomirsky *et al* 2005).

Related to this role, pleasure and pain may also have signatory value because they signal states that have value (see Cabanac 1992; Scherer *et al* 2006). Pleasure occurs in states that promote or constitute evolutionary fitness in a natural environment; pain signifies states that represent poor evolutionary fitness (Fraser & Duncan 1998). On this model, pleasure and lack of pain are more like 'awards' than 'rewards'.

It should be noted at this point that, from the perspective of *scientists*, pleasure and pain cannot be seen directly (cf Ryle 1946/1990; Wittgenstein 1953; Wemelsfelder 1997, 2001). Welfare scientists rely on indicators such as facial expressions (Darwin 1872; Grill & Norgren 1978), vocalisations (Knutson *et al* 2002), play (Blackshaw *et al* 1997; Fraser & Duncan 1998; Spinka *et al* 2001; Webster 2005) and physiological markers of pleasure (Boissy *et al* 2007; Yeates & Main 2008) and pain (Gregory 2004). Such indicators always have signatory value, even for experiences-based approaches to animal welfare. This means that within fitness-based approaches, indicators of pleasure signify something with signatory value. This additional step can make assessment of fitness through inferring pleasure and pain unreliable (Schlesinger 1974; cf Hyslop & Jackson 1972). Consequently, more directly observable measures of fitness will usually be more useful for scientific experiments trying to assess fitness. Nevertheless, there may be cases when inferring pleasure/pain will be practically useful. For example, while syringomyelia may be diagnosed through more direct methods, such as an MRI scan (Rusbridge *et al* 2006), pain-related behaviour can be a more practically useful sign (Rusbridge 2007).

Implications of the value of pleasure and pain

The difference between pleasure and pain's intrinsic value within experiences-based approaches and their extrinsic value within fitness-based approaches entail other differences between fitness-based approaches and experiences-based approaches, summarised in Table 1.

Experiences-based and fitness-based approaches will disagree concerning whether pain is valued positively or negatively. Experiences-based approaches value pain negatively (unless it prevents greater pain). But, within fitness-based approaches, adaptive pain has *positive* contributory and instrumental value. For example, pain has positive instrumental value because it leads to increased fitness, which for fitness-based approaches means higher welfare.

In contrast, the *signatory* value of adaptive pain within fitness-based approaches is negative, because pain signifies a state of unfitness (eg injury, disease). This makes considering signatory value a constructive way for fitness-based approaches to conceptualise pleasure/pain in a way that agrees with experiences-based approaches.

Another difference is that, while experiences-based approaches will consider pleasure and pain to always

Table 1 Value of health, pleasure and pain when matched or mismatched to environments, within experiences-based, fitness-based and naturalness-based approaches to animal welfare (blank spaces represent no necessary value).

	Pleasure				Pain		
	Health	Adaptive in natural environment	Maladaptive in environment	Adaptive in unnatural environment	Adaptive in natural environment	Maladaptive in environment	Adaptive in unnatural environment
<i>Experiences-based</i>	Positive	Positive	Positive	Positive	Negative	Negative	Negative
	Positive						
<i>Fitness-based</i>							
Intrinsic value	Positive						
Instrumental value		Positive	Negative	Positive	Positive	Negative	Positive
Signatory value		Positive		Positive	Negative		Negative
<i>Naturalness-based</i>		Positive	Negative	Negative	Positive	Negative	Negative

have value, in fitness-based approaches the value of affect is contingent on whether or not it is adaptive. Pleasure and pain may not be adaptive. As examples, the self-stimulation of ‘pleasure centres’ (Olds & Forbes 1981; Shizgal 1997) can condition behaviour in ways that fail to increase fitness, or may even be maladaptive (Woolf & Salter 2000; Spruijt *et al* 2001), and place-preference conditioning through electric shocks or the self-administration of opioids (van Ree *et al* 1999; Burgdorf & Panksepp 2006) need not lead to the animal going to places that actually confer greater fitness. Pain may also be maladaptive because the animal cannot respond appropriately, leading to stress, decreased food intake etc, without any advantages in terms of avoiding injury. Thus, depending on the context, pleasure and pain may have positive value, negative value or no value.

The signatory value of pleasure and pain is also contingent on whether they accurately reflect the environment. If the animal’s affective system is somehow subverted from its ideal function so that it ‘mismatches’ the environment, then it may signal incorrectly. For example, stereotypies are characterised by opioid release but this pleasure cannot be taken to accurately signify a state of fitness — indeed, it is suggestive of present or past unfitness (Danzer 1991; Mason 1991a,b). Similarly, in animals that have had effective analgesia, a lack of pain does not signify lack of injury (indeed, self-administration of analgesia may signify pathology; Danbury *et al* 2000). In situations where a mismatch is suspected, pleasure and pain are therefore less trustworthy as signs of fitness or unfitness.

A mismatch between the animal’s affective system and its environment may occur for two reasons. Some mismatches are due to the affective system deviating from its natural evolutionary functioning, ie when it ‘malfunctions’. This is the case for murine models and human patients with congenital insensitivities to pain, fibromyalgia, phantom limb pains or hypersensitivity syndromes in which pain does not correspond to physical injury.

Mismatches may also occur because the environment deviates from the one in which the animal’s affective system has evolved to function. As an extreme example, an animal could be in a virtual reality machine in which it has a perfectly pleasurable life completely disconnected from reality (see Nozick 1974). Any pleasure in this machine would not accurately signify fitness. Similarly, the intra-cranial stimulation of an animal’s ‘pleasure system’ (Heath 1972), would not necessarily signify greater fitness.

When a natural animal is in the natural environment for which it has evolved, such mismatches might be expected to be less likely. A wild animal’s affective system has evolutionarily adapted in a way that ‘matches’ the states likely to occur in its ecological niche. So its affective system is likely to function optimally (or at least satisfactorily) in that environment. In comparison, if the animal or the environment is ‘unnatural’, then mismatches are more likely.

It is not possible, however, to assume that a deviation in affective system from the evolutionary norm *and* a deviation in the environment from the animal’s ecological niche would lead to a greater mismatch than if one or both were ‘natural’. As a (colourful) analogy, if two colours match, one cannot expect that only changing one will be less likely to lead to a clash than changing both.

Applications to breeding for pleasure

Experiences-based approaches to animal welfare would suggest that breeding programmes should aim to breed animals that experience more pleasure and/or less pain (eg Rollin 1995; Sandøe *et al* 1999; McGreevy 2007). This would include breeding healthier animals, since these will experience less pain (ie health has instrumental value in experiences-based approaches). Similarly, experiences-based approaches would support breeding animals that have a greater capacity for pleasure and a lower capacity for pain. For example, it would be a refinement for experiments involving injuries to use animals bred to have lower capac-

Table 2 Whether approaches would support or oppose breeding strategies for natural or altered capacities for pain and pleasure.

	Breeding for increased capacity for pleasure or decreased capacity for pain compared to natural animal		Breeding for natural capacities		Breeding for decreased capacity for pleasure or increased capacity for pain compared to natural animal	
	In natural environment	In unnatural environment	In natural environment	In unnatural environment	In natural environment	In unnatural environment
Experiences-based	Support	Support	Oppose	Oppose	Oppose	Oppose
Fitness-based	Oppose	Support (to match environment)	Support	Oppose	Oppose	Support (to match environment)
Naturalness-based	Oppose	Oppose	Support	Support	Oppose	Oppose

ities for pain (ie lower ‘neurophysiological sensitivity’; European Directive 86/609/EEC, Article 7[3]; Animals [Scientific Procedures] Act 1986 s5[a]). In some cases, where the benefits of making the animals unable to feel pain outweigh the disadvantages of being unable to feel pleasure, experiences-based approaches would therefore legitimise the breeding of insentient ‘hedonic zombie’ animals.

Fitness-based and naturalness-based approaches may agree or disagree about the practical questions (summarised in Table 2).

Signatory value

Considering first the signatory value of pleasure and pain within fitness-based approaches to animal welfare, changes that make animals experience more pleasure and less pain will generally signify that these animals are fitter, and so would be supported by fitness-based approaches. This includes breeding programmes that improve animals’ health without altering their affective systems. This represents a significant area of agreement between fitness-based and experiences-based approaches.

However, because of the contingent nature of signatory value, this argument applies only when the animals’ affective systems and environments are matched. When there is a mismatch between the animal and its environment, the signatory value of pleasure and pain can no longer be trusted as an accurate indicator. For example, if an animal is on high levels of analgesia, under anaesthetic, acyngulate, receiving intracranial stimulation or in a virtual reality machine, and therefore experiences high levels of pleasure or low levels of pain, this does not mean that it is fit.

This conclusion has wider implications regarding other indicators of welfare, where breeding has altered the capacity for the expression of those indicators. For example, the productivity of ‘naturally bred’ animals may generally have positive signatory value because fitter natural animals may be expected to produce more. However, if animals are *bred for* higher productivity, then any increased production cannot be trusted as representing greater fitness. Thus, milk yield may indicate fitness in cows that have not been selected for milk production, but for ‘high genetic merit’ cows that will ‘milk off their own back’, productivity is not a trustworthy indicator.

Instrumental value

In considering the instrumental value of adaptive pain, fitness-based approaches are likely to disagree with experiences-based approaches by opposing the breeding of animals with reduced sensitivity to pain compared to natural types. This would usually be expected to decrease the animals’ fitness, eg by making them predisposed to self-mutilation and injuries (Schulman *et al* 2001; Suriu *et al* 2009). Indeed, in some cases, fitness might be increased by breeding animals with *greater* sensitivity to pain — such animals might have even lower susceptibilities to injury, for example through enhanced allodynia and faster learning. In these cases, an equal or greater capacity for pain would be adaptive and therefore would be promoted, all else being equal, by fitness-based approaches. This is a stark disagreement with experiences-based approaches.

However, this again does not necessarily apply in cases where pain would be maladaptive. Fitness-based approaches would support breeding-out of pain that is maladaptive in the animal’s actual environment (or to alter the environment). For animals whose pain serves no function because they cannot act upon it, or where pain leads to major effects on the animal’s stress and health, breeding programmes could breed out this maladaptive pain. This is analogous to the argument for breeding-out visual abilities where this is expected to increase fitness (for example, by decreasing feather-pecking). In very rare cases, an animal may even be fitter overall if it was insentient. In such situations, fitness-based approaches may agree with experiences-based approaches.

Similar arguments could apply to breeding animals for altered capacities for experiencing pleasure. Fitness would be increased by breeding for adaptive pleasure, but where pleasure is maladaptive, fitness-based approaches would support breeding for lower capacities for pleasure, including insentience.

In both of these cases, maximising the contributory and instrumental value of pleasure and pain is achieved by ‘matching’ the animals’ affective systems to their environment. When animals are to be kept in natural environments, this match is likely to be achieved by breeding natural

animals, eg by using natural methods of selection. Conversely, for ‘natural animals’, such as wild-caught animals, this provides a reason to increase the naturalness of environments from fitness-based approaches. These suggestions provide one area in which fitness-based and naturalness-based approaches will agree about encouraging natural breeding programmes or natural environments. Indeed, generalising between pleasure and pain, all of an animal’s body-systems will have evolved to match its natural environment, and so will have maximal instrumental value in natural systems. Thus, both fitness-based and naturalness-based approaches will agree that there are reasons against releasing domestic species into the wild.

However, while fitness-based approaches would support animals *and* environments both being natural, it may not support *either* being natural on its own. Many domestic species are already very different to their natural types, and most environments highly artificial. In such cases, making only the animals or only the environment more natural may actually lead to a greater mismatch, and thereby decrease fitness. This argument could go further: when environments are unnatural, animals *should* be unnaturally bred with appropriately altered affective systems to reduce this mismatching, where possible. This would disagree strongly with naturalness-based approaches.

Naturalness

To complete the comparison between approaches, naturalness-based and experiences-based approaches may agree that a natural capacity for pleasure is valuable and an unnaturally high capacity for pain has negative value.

Beyond this, experiences-based approaches will not necessarily agree with naturalness-based approaches that natural capacities have greater value than altered capacities. There is no reason to expect that animals having natural affective systems will have the least pleasure and most pain. Evolution is likely to optimise the animals’ capacity for pain in terms of increasing their instrumental value for fitness, rather than in terms of minimising the amount of pain an animal will experience. Therefore, anthropogenic breeding pressures might actually decrease pain or increase pleasure relative to natural breeding.

The same logic applies to animals’ environments. There is no reason to expect *a priori* that a more natural environment will lead to more pleasure and less pain. Clearly it will lead to less pain than ‘hurtful’ unnatural environments, and it could be argued that many intensive farming systems are more hurtful than natural environments. But, in this statement, the term ‘unnatural’ adds nothing: it is the fact that these are hurtful that makes them cause pain. Other unnatural environments (perhaps loving companion animal homes or a virtual reality machine) are unnatural but could provide more pleasure and less pain than natural environments. Again, greater pleasure and less pain may ensue if the environment is made more artificial, especially when animals are highly unnatural (eg some strains of mouse, broiler breeders and some dog breeds).

Thus from a fitness-based or experiences-based approach, it is equally important to assess the state of naturally bred animals in natural environments as it is to assess the state of artificially bred animals in unnatural environments, since there may be scope to improve their welfare.

Animal welfare implications and conclusion

This paper has demonstrated how different approaches in animal welfare can agree and disagree philosophically and practically. All three approaches consider natural, adaptive pleasure as having positive value and would oppose the breeding of animals with maladaptive increased capacities for pain. In addition, all three approaches would generally support breeding strategies that decrease diseases caused by unnatural breeding regimes. This constitutes a major area of common ground.

Where the different approaches disagree about altering animals’ affective systems, the practical conclusions a reader may draw from this paper depend on the approach they take to animal welfare. If one takes an experiences-based approach, then animals should be kept and bred to maximise pleasure, and breeding unnatural animals, including insentient ‘hedonic zombies’ and creating unnatural environments may often seem a good idea. If one takes a fitness-based or naturalness-based approach, then environmental design and breeding should aim for fitness or naturalness, and accept that this may lead to animals that experience less pleasure and more pain.

If one takes a pluralistic approach, then one will have to resolve the differences between the approaches that are included in the pluralistic approach. For example, Webster’s definition may have to decide whether animals in an unnatural environment should be bred to have a lower capacity for pain (which may make them happier but less fit) or a natural capacity for pain (which may make them fitter but less happy).

It is hoped that this paper helps individuals to decide how they view animal welfare. It is also hoped that highlighting the agreements and disagreements will assist and encourage co-operation between the different philosophical approaches to animal welfare, and help the development of pluralist practical approaches. In many cases this will have practical benefits, ultimately increasing animal welfare — from whatever approach.

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References

- Allen C and Beckoff M** 2007 Animal minds, cognitive ethology and ethics. *The Journal of Ethics* 11: 299-317
- Appleby MC and Sandøe P** 2002 Philosophical debate on the nature of well-being: implications for animal welfare. *Animal Welfare* 11(3): 283-294
- Baars BJ** 2002 The conscious access hypothesis: origins and recent evidence. *Trends in Cognitive Sciences* 6: 47-52
- Belknap JK, Haltli NR, Goebel DM and Lamé M** 1983 Selective breeding for high and low levels of opiate-induced analgesia in mice. *Behavior Genetics* 13: 383-396
- Berridge KC** 1996 Food reward: brain substrates of wanting and liking. *Neuroscience and Biobehavioural Reviews* 20(1): 1-25
- Berridge KC** 2003 Pleasures of the brain. *Brain and Cognition* 52: 106-128
- Berridge KC and Robinson TE** 2003 Parsing reward. *Trends in Neuroscience* 26: 507-513
- Berridge KC and Winkielman P** 2003 What is an unconscious emotion? (The case for unconscious 'liking'). *Cognition Emotion* 17: 181-211
- Blackshaw JK, Swain AJ, Blackshaw AW, Thomas FJM and Gillies KJ** 1997 The development of playful behaviour in piglets from birth to weaning in three farrowing environments. *Applied Animal Behaviour Science* 55: 37-49
- Boden MA** 1990 Escaping from the Chinese room. In: Boden MA (eds) *The Philosophy of Artificial Intelligence* pp 89-104. Oxford University Press: Oxford, UK
- Boissy A, Manteuffel G, Jensen MB, Moe RO, Spruijt B, Keeling LJ, Winckler C, Forkman B, Dimitrovi I, Langbein J, Bakken M, Veissier I and Aubert A** 2007 Assessment of positive emotions in animals to improve their welfare. *Physiology and Behavior* 92: 375-397
- Bracke MBM and Hopster H** 2006 Assessing the importance of natural behaviour for animal welfare. *Journal of Agricultural and Environmental Ethics* 19: 77-89
- Bradley B** 1998 Extrinsic value. *Philosophical Studies* 91: 109-126
- Breslin PA, Spector AC and Grill HJ** 1992 A quantitative comparison of taste reactivity behaviours to sucrose before and after lithium chloride pairings: A unidimensional account of palatability. *Behavioural Neuroscience* 106: 820-836
- Broom DM** 1988 The scientific assessment of animal welfare. *Applied Animal Behaviour Science* 20: 5-19
- Broom DM** 1998 Welfare, stress and the evolution of feelings. *Advances in the Study of Behaviour* 27: 371-403
- Broom DM** 2007 Quality of life means welfare: How is it related to other concepts and assessed? *Animal Welfare* 16: S45-S53
- Broom DM and Johnson K** 1993 *Stress and Animal Welfare*. Kluwer Academic Publishers: Dordrecht, The Netherlands
- Burgdorf J and Panksepp J** 2006 The neurobiology of positive emotions. *Neuroscience and Biobehavioural Reviews* 30: 173-187
- Burman OHP, Parker R, Paul ES and Mendl M** 2008 A spatial judgement task to determine background emotional state in laboratory rats, *Rattus norvegicus*. *Animal Behaviour* 76: 801-809
- Cabanac M** 1971 Physiological role of pleasure. *Science* 173: 1103-1107
- Cabanac M** 1979 Sensory pleasure. *Quarterly Review of Biology* 54: 1-29
- Cabanac M** 1992 Pleasure: the common currency. *Journal of Theoretical Biology* 155: 173-200
- CAWC** 2008 Fixing ancestral problems: genetics and welfare in companion animals focusing on syringomyelia in Cavalier King Charles Spaniels as an example. *Report of the Companion Animal Welfare Council Workshop*. 29th April 2008. House of Lords, London, UK
- Chalmers D** 1996 *The Conscious Mind*. Oxford University Press: Oxford, UK
- Damasio AR** 1994 *Descartes' Error: Emotion, Reason and the Human Brain*. Picador: London, UK
- Danbury TC, Weeks CA, Waterman-Pearson AE, Kestin SC and Chambers JP** 2000 Self-selection of the analgesic drug carprofen by lame broiler chickens. *Veterinary Record* 146(11): 307-311
- Dantzer R** 1991 Stress, stereotypies and welfare. *Behavioural Processes* 25: 95-102
- Darwin C** 1872 *The Expressions of the Emotions in Man and Animals*. Longmans: London, UK
- Dawkins MS** 1988 Behavioural deprivation: a central problem in animal welfare. *Applied Animal Behaviour Science* 20: 209-225
- Dawkins MS** 1990 From an animal's point of view: motivation, fitness and animal welfare. *Behavioral and Brain Sciences* 13: 1-60
- Dawkins MS** 1998 Evolution and animal welfare. *Quarterly Review of Biology* 73: 305-328
- Dawkins MS** 2000 Animal minds and animal emotions. *American Zoologist* 40: 883-888
- Dawkins MS** 2001 Who needs consciousness? *Animal Welfare* 10: S19-S32
- Dawkins MS** 2003 Behaviour as a tool in the assessment of animal welfare. *Zoology* 106(4): 383-387
- Dawkins MS** 2005 The science of suffering. In: McMillan FD (ed) *Mental Health and Wellbeing in Animals* pp 47-56. Blackwell: Ames, USA
- D'Eath RB, Lawrence AB, Conington J, Olsson IAS and Sandøe P** 2010 Breeding for behavioural change in farm animals: practical and ethics considerations. *Animal Welfare* 19: S17-S27
- Dearborn GVN** 1932 A case of congenital pure analgesia. *Journal of Nervous and Mental Disease* 75: 612-615
- DeGrazia D** 1998 Wellbeing of animals. In: Beckoff M and Meany CA (eds) *Encyclopedia of Animal Rights and Animal Welfare* pp 359-360. Greenwood Press: Westport, USA
- Désiré L, Boissy A and Veissier I** 2002 Emotion in farm animals: a new approach to animal welfare in applied ethology. *Behavioural Processes* 60: 165-180
- Duncan I** 1993 Welfare is to do with what animals feel. *Journal of Agricultural & Environmental Ethics* 6(2): S8-S14
- FAWC (Farm Animal Welfare Council)** 1998a *Report on the Welfare of Broiler Breeders*. FAWC: London, UK
- FAWC (Farm Animal Welfare Council)** 1998b *Report on the Implications of Cloning for the Welfare of Farmed Livestock*. FAWC: London, UK
- Feldman F** 1986 *Doing the Best We Can: An Essay in Informal Deontic Logic*. D. Reidel: Dordrecht, The Netherlands
- Feldman Barrett L and Russell JA** 1998 Independence and bipolarity in the structure of current affect. *Journal of Personality and Social Psychology* 74: 967-984
- Filligim RB, Wallace MR, Herbstman DM, Ribeiro-Dasilva M and Staud R** 2009 Genetic contributions to pain: a review of findings in humans. *Oral Diseases* 14: 673-682
- Frankena WK** 1963 *Ethics*. Prentice Hall: Englewood Cliffs, USA
- Fraser D** 1995 Science, values and animal welfare: exploring the 'inextricable connection'. *Animal Welfare* 4: 103-117
- Fraser D** 1998 Animal Welfare. In: Beckoff M and Meany CA (eds) *Encyclopedia of Animal Rights and Animal Welfare* pp 55-57. Greenwood Press: Westport, USA
- Fraser D and Duncan IJ** 1998 'Pleasures', 'pains' and animal welfare: toward a natural history of affect. *Animal Welfare* 7: 383-396
- Fraser D, Weary DM, Pajor EA and Milligan BN** 1997 A scientific concept of animal welfare that reflects ethical concerns. *Animal Welfare* 6: 187-205
- Gregory NG** 2004 *Physiology and Behaviour of Animal Suffering*. UFAW/Blackwell: Oxford, UK

- Grill HJ and Norgren R** 1978 The taste reactivity test I. Mimetic responses to gustatory stimuli in neurologically normal rats. *Brain Research* 143: 263-279
- Gross JJ, John OP and Richards JM** 2000 The dissociation of emotion expression from emotion experience: A personality perspective. *Personality and Social Psychology Bulletin* 26: 712-726
- Harding E, Paul ES and Mendl M** 2004 Cognitive bias and affective state. *Nature* 427: 312
- Harrison P** 1989 Theodicy and animal pain. *Philosophy* 64: 79-92
- Hassenbusch SJ, Pillay PK and Barnett GH** 1990 Radiofrequency cingulotomy for intractable cancer pain using stereotaxis guided by magnetic resonance imaging. *Neurosurgery* 27: 220-223
- Hauser L** 1993 Reaping the whirlwind: reply to Harnad's other bodies, other minds. *Minds and Machines* 3: 219-238
- Heath RG** 1972 Pleasure and brain activity in man. *Journal of Nervous and Mental Disease* 154: 3-18
- Heeger R and Brom FWA** 2001 Intrinsic value and direct duties: from animal ethics towards environmental ethics. *Journal of Agricultural and Environmental Ethics* 14: 241-252
- Hinde RA** 1985 Was 'the expression of the emotions' a misleading phrase? *Animal Behaviour* 33: 985-992
- Hornemann T, Penno A, Richard S, Nicholson G, van Dijk FS, Rothier A, Timmerman V and von Eckardstein A** 2009 A systematic comparison of all mutations in hereditary sensory neuropathy type I (HSAN I) reveals that the G387A mutation is not disease associated. *Neurogenetics* 10: 135-143
- Hyslop A and Jackson FC** 1972 The analogical inference to other minds. *American Philosophical Quarterly* 9(2): 168-176
- Indo Y, Tsurata Y, Karim MA, Ohta K, Kawano T, Mitsubuchi H, Tonoki H, Awaya Y and Matsuda I** 1996 Mutations in the TRKA/NGF receptor gene in patients with congenital insensitivity to pain with anhidrosis. *Nature Genetics* 13: 485-488
- Jestic JV, Urry PA and Efthimiou J** 1985 An hereditary sensory and autonomic neuropathy transmitted as an X-linked recessive trait. *Journal of Neurology, Neurosurgery, and Psychiatry* 48: 1259-1264
- Jones RB and Hocking PM** 1999 Genetic selection for poultry behaviour: big bad wolf or friend in need? *Animal Welfare* 8(4): 343-359
- Kanis E, De Greef KH, Hiemstra A and van Arendonk JAM** 2005 Breeding for societally important traits in pigs. *Journal of Animal Science* 83: 948-957
- Kelley AE, Baldo BA, Pratt WE and Will MJ** 2005 Corticostriatal-hypothalamic circuitry and food motivation: Integration of energy, action and reward. *Physiology and Behaviour* 86: 773-795
- Knutson B, Burgdorf J and Panksepp J** 2002 Ultrasonic vocalisations as indices of affective states in rats. *Psychological Bulletin* 128: 961-977
- Korsgaard C** 1983 Two distinctions in goodness. *Philosophical Review* 92: 169-195
- LaCroix-Fralish ML and Mogil JS** 2009 Progress in genetic studies of pain and analgesia. *Annual Review of Pharmacology and Toxicology* 49: 97-121
- Lane RD, Ahern GL, Schwarz GE and Kasniak AW** 1997 Is alexithymia the emotional equivalent of blindsight? *Biological Psychiatry* 42: 834-844
- Lawrence AB, Conington J and Simm G** 2004 Breeding and animal welfare: practical and theoretical advantages of multi-trait selection. *Animal Welfare* 13: S191-S196
- Lerner JS and Keltner D** 2000 Beyond valence: Toward a model of emotion-specific influence on judgement and choice. *Cognition Emotion* 14: 473-493
- Lewis CI** 1955 *The Ground and Nature of the Right*. Columbia University Press: New York, USA
- Lindahl BIB** 1997 Consciousness and biological evolution. *Journal of Theoretical Biology* 187: 613-626
- Lund V, Coleman G, Gunnarsson S, Appleby MC and Karkinen K** 2006 Animal welfare science. Working at the interface between the natural and social sciences. *Applied Animal Behaviour Science* 97: 37-49
- Lundberg R** 1985 What kind of good is a kind and caring heart? *Journal of Value Inquiry* 19: 119-131
- Lykken D and Tellegen A** 1996 Happiness is a stochastic phenomenon. *Psychological Science* 7: 186-189
- Lyubomirsky S, King L and Diener E** 2005 The benefits of frequent positive affect: does happiness lead to success? *Psychological Bulletin* 131: 803-855
- MacArthur Clark JA, Potter M and Harding E** 2006 The welfare implications of animal breeding and breeding technologies in commercial agriculture. *Livestock Science* 103: 270-281
- Mason G** 1991a Stereotypies: a critical review. *Animal Behaviour* 41: 1015-1037
- Mason GJ** 1991b Stereotypies and suffering. *Behavioural Processes* 25: 103-115
- Mason G and Mendl M** 1993 Why is there no simple way of measuring animal welfare? *Animal Welfare* 2: 301-319
- McGreevy PD** 2007 Breeding for quality of life. *Animal Welfare* 16: S125-S128
- McGreevy PD and Nicholas FW** 1999 Some practical solutions to welfare problems in dog breeding. *Animal Welfare* 8: 329-341
- McMillan FD** 2003 Maximising quality of life in ill animals. *Journal of the American Animal Hospital Association* 39: 227-235
- Meadows ME and Kaplan RF** 1994 Dissociation of autonomic and subjective responses to emotional slides in right hemisphere damaged patients. *Neuropsychologia* 32: 847-856
- Mogil JS** 1999 The genetic mediation of individual differences in sensitivity to pain and its inhibition. *Proceedings of the National Academy of Sciences* 96: 7744-7751
- Mogil JS, Wilson SG, Bon K, Lee SE, Chung K, Raber P, Pieper JO, Hain HS, Belknap JK, Hubert L, Elmer GI, Chung JM and Devor M** 1999a Heritability of nociception I. Responses of eleven inbred mouse strains on twelve measures of nociception. *Pain* 80: 67-82
- Mogil JS, Wilson SG, Bon K, Lee SE, Chung K, Raber P, Pieper JO, Hain HS, Belknap JK, Hubert L, Elmer GI, Chung JM and Devor M** 1999b Heritability of nociception II. 'Types' of nociception revealed by genetic correlation analysis. *Pain* 80: 83-93
- Mogil JS, Yu L and Basbaum AI** 2000 Pain genes? Natural variation and transgenic mutants. *Annual Review of Neuroscience* 23: 777-811
- Moody T** 1994 Conversations with zombies. *Journal of Consciousness Studies* 1: 196-200
- Morgan CL** 1984 *An Introduction to Comparative Psychology*. Walter Scott: London, UK
- Nauta WJ, Baars T, Saatkamp H, Weenink D and Roep D** 2009 Farming strategies in organic dairy farming: effects on breeding goal and choice of breed. An explorative study. *Livestock Science* 121: 187-199
- Nielsen CS, Stubhaug A, Price DD, Vassend O, Czajkowski N and Harris JR** 2008 Individual differences in pain sensitivity: genetic and environmental contributions. *Pain* 136: 21-29
- Norbury TA, MacGregor AJ, Urwin J, Spector TD and McMahon SB** 2007 Heritability of responses to painful stimuli in women: a classical twin study. *Brain* 130: 3041-3049

- Nordenfelt L** 2006 *Animal and Human Health and Welfare: A Comparative Philosophical Analysis*. CABI: Wallingford, UK
- Nozick R** 1974 *Anarchy, State and Utopia*. Blackwell: Malden, MA, USA
- Oertel B and Lötsch J** 2008 Genetic mutations that prevent pain: implications for future pain medication. *Pharmacogenomics* 9(2): 179-194
- Olds ME and Forbes JL** 1981 The central basis of motivation: intracranial self-stimulation studies. *Annual Review of Psychology* 32: 523-574
- Olsson IAS, Gamborg C and Sandøe P** 2005 Taking ethics into account in farm animal breeding: what can breeding companies achieve? *Journal of Agricultural and Environmental Ethics* 19: 37-46
- O'Neill J** 1992 The varieties of intrinsic value. *Monist* 75: 119-137
- Panksepp J** 1994 Evolution constructed the potential for subjective experience within the neurodynamics of the mammalian brain. In: Ekman P and Davidson RJ (eds) *The Nature of Emotion: Fundamental Questions* pp 396-399. Oxford University Press: Oxford, UK
- Panksepp J and Burgdorf J** 2000 50-kHz chirping (laughter?) in response to conditioned and unconditioned tickle-induced reward in rats: effects of social housing and genetic variables. *Behavioural and Brain Research* 115: 25-38
- Panocka I, Marek P and Sadowski B** 1986 Inheritance of stress-induced analgesia in mice. Selective breeding study. *Brain Research* 397: 152-155
- Popper KR** 1978 Natural selection and the emergence of mind. *Dialectica* 32: 339-355
- Pressman S and Cohen S** 2005 Does positive affect influence health? *Psychological Bulletin* 131: 925-971
- Rabinowicz W and Rønnow-Rasmussen T** 1999 A distinction in value: intrinsic and for its own sake. *Proceedings of the Aristotelian Society* 100: 33-52
- Rauw WM, Kanis E, Noordhuizen-Stassen EN and Grommers FJ** 1998 Undesirable side effects of selection for high production efficiency in farm animals: as review. *Livestock Production Science* 56: 15-33
- Rollin BE** 1995 *The Frankenstein Syndrome: Ethical and Social Issues in the Genetic Engineering of Animals*. Cambridge University Press: Cambridge, UK
- Rusbridge C** 2007 *Chiari-like malformation and syringomyelia in the Cavalier King Charles spaniel*. PhD dissertation, University of Utrecht. Available at <http://igitur-archive.library.uu.nl/dissertations/2007-0320-201201/full.pdf>
- Rusbridge C, Greitz D and Iskandar BJ** 2006 Syringomyelia: current concepts in pathogenesis, diagnosis, and treatment. *Journal of Veterinary Internal Medicine* 20(3): 469-479
- Ryle G** 1946/1990 *The Concept of Mind*. Penguin: London, UK
- Sandøe P** 1999 Quality of life, three competing views. *Ethical Theory and Moral Practice* 2: 11-23
- Sandøe P, Christiansen SB and Appleby MC** 2003 Farm animal welfare: the interaction of ethical questions and animal welfare science. *Animal Welfare* 12: 469-478
- Sandøe P, Holtug N and Simonsen HB** 1996 Ethical limits to domestication. *Journal of Agricultural and Environmental Ethics* 9: 114-122
- Sandøe P, Nielsen BL, Christensen LG and Sørensen P** 1999 Staying good while playing God. The ethics of breeding farm animals. *Animal Welfare* 8: 313-328
- Sandøe P and Simonsen HB** 1992 Assessing animal welfare: where does science end and philosophy begin? *Animal Welfare* 1: 257-267
- Scherer KR, Dan ES and Flykt A** 2006 What determines a feeling's position in affective space? A case for appraisal. *Cognition and Emotion* 20(1): 92-113
- Schlesinger G** 1974 Induction and other minds. *Australian Journal of Philosophy* 52(1): 3-21
- Schulman H, Tsodikow V, Einhorn M, Lecy Y, Shorer Z and Hertzanu Y** 2001 Congenital insensitivity to pain with anhidrosis (CIPA): the spectrum of radiological findings. *Pediatric Radiology* 31: 701-705
- Searle J** 1984 *Minds, Brains & Science: The 1984 Reith Lectures*. Penguin Books: London, UK
- Seth AK, Baars BJ and Edelman DB** 2005 Criteria for consciousness in humans and other mammals. *Consciousness and Cognition* 14: 119-139
- Sherwin C** 2001 Can invertebrates suffer? Or, how robust is argument by analogy? *Animal Welfare* 10: S103-S118
- Shir Y, Zeltser R, Vatine JJ, Carmi G, Belfer I, Zangen A, Overstreet D, Raber P and Seltzer Z** 2001 Correlation of intact sensibility and neuropathic pain-related behaviors in eight inbred and outbred rat strains and selection lines. *Pain* 90: 75-82
- Shizgal P** 1997 Neural basis of utility estimation. *Current Opinion in Neurobiology* 7(2): 198-208
- Smeyne RJ, Klein R, Schnapp A, Long LK, Bryant S, Lewin A, Lira SA and Barbacid M** 1994 Severe sensory neuropathies in mice carrying a disrupted Trk/NGF receptor gene. *Nature* 368: 246-249
- Smith JW** 1948 Intrinsic and extrinsic good. *Ethics* 58(3): 195-208
- Spinka M, Newbury RC and Bekoff M** 2001 Mammalian play: training for the unexpected. *Quarterly Review of Biology* 76: 141-168
- Spruijt BM, van den Bos R and Pijlman FTA** 2001 A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Applied Animal Behaviour Science* 72: 145-171
- Suriu C, Khayat M, Weiler M, Kfir N, Cohen C, Zinger A, Aslanidis C, Schmitz G and Falik-Zaccai TC** 2009 Skoura, a genetic island for congenital insensitivity to pain and anhidrosis among Moroccan Jews, as determined by a novel mutation in the NTRK1 gene. *Clinical Genetics* 75: 230-236
- Tannenbaum J** 1991 Ethics and animal welfare: the inextricable connection. *Journal of the American Veterinary Medical Association* 198: 1360-1376
- Thrush DC** 1973 Congenital insensitivity to pain: a clinical, genetic and neurophysiological study of four children from the same family. *Brain* 96: 369-386
- UFAW** 2009 *Genetic Welfare Problems of Companion Animals: Syringomyelia in the Cavalier King Charles Spaniel*. Available at <http://www.ufaw.org.uk/syring.php>
- van Ree JM, Gerrits MAFM and Vandershuren LJM** 1999 Opioids, reward and addiction: an encounter of biology, psychology and medicine. *Pharmacological Reviews* 51: 341-396
- Verhagen JV and Engelen L** 2006 The neurocognitive bases of human multimodal food perception. *Neuroscience and Biobehavioural Reviews* 30: 613-650
- Webster J** 2005 *Animal Welfare: Limping Towards Eden*. UFAW/Blackwell: Oxford, UK
- Wechsler B** 1995 Coping and coping strategies: A behavioural view. *Applied Animal Behaviour Science* 43: 123-134
- Wechsler B and Lea SEG** 2007 Adaptation by learning: Its significance for farm animal husbandry. *Applied Animal Behaviour Science* 108: 197-214
- Wemelsfelder F** 1997 The scientific validity of subjective concepts in models of animal welfare. *Applied Animal Behaviour Science* 53: 75-88
- Wemelsfelder F** 2001 The inside and outside aspects of consciousness: complementary approaches to the study of animal emotion. *Animal Welfare* 10: S129-S139
- Wilkinson HA, Davidson KM and Davidson RI** 1999. Bilateral anterior cingulotomy for chronic non-cancer pain. *Neurosurgery* 45(5): 1129-1136

Wilson SG and Mogil JS 2001 Measuring pain in the (knock-out) mouse: big challenges in a small mammal. *Behavioural Brain Research* 125: 65-73

Winkelman P and Berridge KC 2004 Unconscious emotion. *Current Directions in Psychological Science* 13: 120-123

Wittgenstein L 1953 *Philosophical Investigations*. Blackwell: Oxford, UK

Wojciechowska JI and Hewson CJ 2005 Quality-of-life-assessment in pet dogs. *Journal of the American Veterinary Medical Association* 226: 722-728

Woolf CJ and Salter MW 2000 Neuronal plasticity: increasing the gain in pain. *Science* 288: 1765-1768

Yeates JW and Main DCJ 2008 Assessment of positive welfare: a review. *The Veterinary Journal* 175: 293-300

Yeates JW and Main DCJ 2009 Assessment of companion animal quality of life in veterinary practice and research. *Journal of Small Animal Practice* 50(6): 274-283

Zald DH and Depue RA 2001 Serotonergic functioning correlates with positive and negative affect in psychiatrically healthy males. *Personality and Individual Differences* 30: 71-86