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# Animal Pleasure and its Moral Significance

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# Animal Pleasure and its Moral Significance

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## ABSTRACT

This paper presents arguments for, and evidence in support of, the important role of pleasure in animals' lives, and outlines its considerable significance to humankind's relationship to other animals. In the realms of animal sentience, almost all scholarly discussion revolves around its negative aspects: pain, stress, distress, and suffering. By contrast, the positive aspects of sentience – rewards and pleasures – have been rarely broached by scientists. Yet, evolutionary principles predict that animals, like humans, are motivated to seek rewards, and not merely to avoid pain and suffering. Natural selection favours behaviours that enhance survival and procreation. In the conscious, sentient animal, the drives to secure food, shelter, social contact, and mates are motivated by desire (appetitive behaviour) and reinforced by pleasure (consummative behaviour). This is reflected in animals' behaviour in the realms of play, food, sex, and touch. Despite the heuristic value of interpreting animal behaviour through the proximate (experiential) lens, scholarly study of animals remains entrenched almost exclusively in the ultimate (evolutionary) sphere. Not just science but also ethics suffer for this, for when we see animals as only the products of a competitive struggle for survival, we risk overlooking the positive qualities of their lives. Pleasure has moral import for such practices as factory farming and laboratory research, for it amplifies the moral burden of depriving animals the opportunity to lead fulfilling, enjoyable lives.

## INTRODUCTION

At long last, sentience is gaining the importance it deserves in matters concerning humans' relationship to other animals. For much of the 20th Century questions of animals' so-called "private" experiences were dismissed as invalid by leading scientific dogma. Today's more enlightened science is entertaining questions of animal consciousness, cognition, emotion, and pain. This is significant, because animals' capacity to suffer has always been at the core

of animal welfare and animal rights ideologies (Bentham, 1789; Singer, 1975). This special issue on animal suffering and welfare is just the latest in a rapidly growing literature on animal sentience.

Intriguingly lacking from this discourse has been animals' capacity for pleasure. With the exception of a few notable contributions (e.g., Cabanac, 1971; Panksepp, 1998), discussions of animal sentience have been almost exclusively in the negative realm: pain, stress, distress. At least nineteen current English language journals (most of them medical) contain the word "pain," whereas none deal with "pleasure." Granted, pain has more moral urgency than does pleasure (see *Pleasure's Moral Significance*, below), the role of pleasure in human and non-human experience nevertheless deserves far more attention than we have been giving it.

This paper aims to help correct this imbalance by presenting the argument for animal pleasure, providing some illustrative examples, and then discussing some of its moral implications. A more thorough examination of animal pleasure can be found in my book *Pleasurable Kingdom: Animals and the Nature of Feeling Good* (also available in German translation as *Tierisch Vergnügt*) (Balcombe, 2006a). The current paper includes some newer ideas and perspectives on animal pleasure and its moral implications since publication of that earlier work.

I should briefly allude to the boundaries of what constitutes an "animal" in the arguments which follow. It is not the intention of this paper to establish where we might draw the line as to what species are sentient. It will be apparent from the examples I give below that I favour a relatively inclusive definition that embraces all vertebrate taxa as well as some invertebrates, such as cephalopod mollusks. For most, the yardstick (if not necessarily the pinnacle) of sentience is likely to be an animal's degree of similarity to humans. What matters for our purposes is that we can agree to include at least some non-human animals here. Few would argue, for instance, that a dog or a giraffe is not sentient.

### **Myopic science**

Science has and continues to hold too narrow a perspective in its scholarly interpretation of animal existence. Specifically, published studies of animal behaviour are presented almost exclusively in an ultimate, evolutionary context, without discussion of the animals' more proximate, mental and emotional experiences. This pattern arises from science's pursuit of rigour, which is assumed to be found primarily in the evolutionary context. Schooled on Occam's Razor, which holds that the explanation of any phenomenon should make as few assumptions as possible, scientists adhere to the law of parsimony like a barnacle to a boat hull. We do not like making assumptions, and we certainly do not wish to be anthropomorphic (Kennedy, 1992).

For example, when rats show a preference for novel flavours following three days pre-exposure to a single flavour, we comfortably propose evolutionary theories to account for the switch. The rats' behaviour appears adaptive for two reasons: (1) it avoids over-dependence on a potentially short-lived food source, and/or (2) it reduces the risk of developing a micronutrient deficiency (Galef and Whiskin, 2003). These are quite sensible adaptive explanations for the rats' behaviour. But we also know with reasonable certainty

that rats do not bone up on Darwinian fitness or ruminate on evolutionary theory. Thus, we take too narrow a view when we fail to acknowledge the likely experiential basis for the rats' behaviour: that they simply got tired of eating the same old fare and enjoyed something new.

Similarly, while there may be good adaptive bases for the broad and diverse human cultural practice of adding spices to our foods (Billings and Sherman, 1998), I am not aware that anyone reaches for the oregano or the curry powder with the conscious intent of warding off intestinal microbes. We spice our food because it enhances the taste.

I propose that Occam's Razor has been blunted by overuse. As evidence of animals' cognitive and emotional capacities snowballs (now that we have ended the embargo on addressing these concepts), it becomes increasingly clear that animals are conscious, experiencing individuals. And it follows that to deny them such experiences – as science tacitly does by neglecting to discuss them – we become increasingly outmoded and anthropocentric, and science loses rigour (Burghardt, 2007). Whenever we address questions about how an animal might be feeling, we inevitably make assumptions because we cannot know absolutely what the animal is feeling. And we inescapably anthropomorphize because we are anthropoid apes. These are not sins so long as we make reasonable assumptions backed by good science, and so long as we anthropomorphize critically, from a foundation of knowledge of the animals we were describing (Burghardt, 1991). In the face of current knowledge, it is a bigger assumption that animals are unconscious, unfeeling things than that they are sentient, emotional and aware. Furthermore, ascribing conscious experience to animals, and the sentience that ensues, need not be seen to violate the law of parsimony, for cognitive explanations can be simpler than cumbersome stimulus–response explanations (de Waal, 1991).

### **ARGUMENTS FOR A PLEASURABLE KINGDOM**

Because an appreciation of animal pleasure and its ethological study –we might call it Hedonic Ethology – is a nascent and as yet under-represented field, it helps to present some arguments for its presence and significance. In addition to the issues of parsimony and anthropomorphism mentioned above, there are still influential scholars who deny animals a conscious experience of life (e.g., Budiansky, 1998; Macphail, 1998; Wynne, 2004). Thus, the argument still needs making.

Before I proceed with the arguments I find to be most compelling for animals' experience of pleasure, let me point out the hypocrisy of any argument for the unprovability of animal conscious experience that nevertheless accepts its existence in humans. In the purest sense, human sentience is no more scientifically provable than is non-human sentience. While our sophisticated language likely permits us to share our pain/pleasure experiences more discretely on the psychological plane than for other taxa, the physical privacy of individual experience is as unbridgeable between two humans as it is between a human and a non-human animal. Quite literally, one person cannot actually feel another's pain or pleasure.

Do we thereby accept the non-existence of human sentience? No. We accept it, and with good reasons even though the solipsist's claim that "my mind is the only thing that I know

exists" is logically incontrovertible. Thus, to accept the existence of sentience in humans while denying it in certain animals (say, birds) is scientifically and ethically inconsistent.

### **Pleasure is adaptive**

Pleasure is a product of evolution. The evolution of motility was a key step towards the eventual evolution of complex sensory systems that could perceive environments and detect noxious and rewarding stimuli. Just as the capacity for pain is adaptive for a mobile organism that can move away from aversive things, so too is pleasure beneficial by rewarding the individual for performing behaviours that promote survival and procreation (Cabanac, 1971). Because animals can actively avoid and approach things, they benefit from being able to have a qualitative experience of those things. Pain's unpleasantness helps steer the animal away from "bad" behaviours that risk the greater evolutionary disaster of death (Dawkins, 1998). Similarly, pleasure encourages animals to behave in "good" ways, such as feeding, mating, and – depending on climatic conditions – staying warm or cool. There are of course energetic costs to evolving and growing complex neurological organs and sensory systems, but clearly the benefits have outweighed the costs, at least for members of Phylum Chordata.

### **Humans feel pleasure**

Arguing the case for animal pleasure would be more difficult were it not for the fact that humans experience pleasure. That we know and accept the existence of this sensory phenomenon in one species provides a foundation for its presumptive existence in others. That human languages contain rich vocabularies for describing good feelings attests to the diversity of both physical and emotional pleasures that can be felt by humans. English includes: happiness, delight, surprise, anticipation, pride, satisfaction, joy, elation, ecstasy, thrill, euphoria, exultation, jubilation, excitement, rapture, fulfillment, gratification, and comfort, among others. Though the writer is unilingual, he is aware of at least one German word – *funktionslust*: the pleasure in what one does best – that captures a sort of pleasure for which English has not a word (Masson and McCarthy, 1995). It seems likely that other languages contain terms for distinctive pleasures.

Having evolved in diverse environments, where different niches present different adaptive challenges and opportunities, different animals have different sensory and perceptual skill sets. It follows that some animals might be able to experience realms of pleasure unfamiliar to humans. The echolocation abilities of bats and cetaceans, electric communication in fishes (Hopkins, 1974), and the ability of pinnipeds to detect fish turbulence trails with their vibrissae (Dehnhardt et al., 2001; Schulte-Pelkum et al., 2007) are representative examples. Some animals can tune into the earth's magnetic field to help navigate, and there is now evidence that birds perceive this visually (Heyers et al., 2007). These examples do not explicitly involve pleasure, but they illustrate the potential for pleasures unknown to us. Two leading neuroscientists, and an ethologist, have recently suggested that other animals may experience some feelings more intensely than we do (Burgdorf and Panksepp, 2007; Bekoff, 2007).

## **Animals feel pain and distress**

A heuristic argument for animals' experience of pleasure is that they feel pain. Pain in animals is well studied, and there is solid empirical evidence for its existence in vertebrate groups (Braithwaite, 2007). The detection of a nociceptive stimulus is highly adaptive for motile organisms that can move away from the source of the stimulus. We can imagine an ancient, primitive animal flinching and fleeing from the bite of another. By escaping more readily than would a non-perceiving conspecific, her genes are more likely to show up in future generations. For animals with highly developed nervous and sensory systems, being able to learn from an earlier painful experience is a further refinement of the stimulus–response dynamic. Cognitive creatures can recognize and remember the source of an earlier hurt, and make adjustments to their behaviour to reduce the chances of a repeat experience. The conscious pain perceiver is once again more likely to survive future encounters and to be favoured by natural selection.

Indirect evidence for animal pain is widespread in nature. Plants, for example, have exploited animals' capacity for pain and discomfort with the evolution of thorns, and bitter tasting chemical compounds in their tissues. Similarly, many animals have well-developed spines, stingers, horns, and tusks which, like thorns, not only inflict pain, but also signal "don't touch."

More direct evidence for animal pain resides in animals' behavioural responses to noxious stimuli. Their vocalizations and their movements – retreating from and avoiding the source of pain, flinching, limping, protecting the injured part – are all consistent with what we may expect of an individual who experiences pain.

Scientific studies of animal pain reinforce what observations suggest. Laboratory studies have shown repeatedly that injured rats will favour the bitter taste of water that contains a pain-relieving drug over unadulterated water (Persinger, 2003; Colpaert et al., 1980, 1982). Chickens also self-administer pain-killers. These birds often experience leg problems associated with breeding, growth and husbandry, and can develop highly abnormal gaits, or become completely unable to walk. Lameness ingests more drugged food than non-lame birds, and as the severity of the lameness increases, lame birds consume a greater proportion of the drugged food (Danbury et al., 2000). Fishes can learn to avoid noxious stimuli such as electric shocks (Ehrensing et al., 1982) and anglers' hooks (Beukema, 1970a,b), and the evidence for fishes' experience of pain is mounting (Braithwaite, 2007). Empirical evidence is now emerging that suggests that some invertebrates experience pain (Elwood, 2007).

## **Animals behave as if they feel pleasure**

### **Play**

Play behaviour is widespread in mammals, and has also been described in about half of all avian families (Ortega and Bekoff, 1987). Behaviour suggesting play has been also observed in other taxa, including reptiles, fishes, and cephalopods (see Burghardt, 2005). Because play tends to occur spontaneously and unpredictably, it is difficult to measure, and most published studies of animal play are anecdotal. While the accumulation of well-documented

anecdotes has scientific value, there is also a growing database of empirical studies of play. For example, a three-year study of aerial drop-catching behaviour by Herring Gulls in Virginia concluded that it was play. These birds will drop clams onto hard surfaces to smash them and access the soft parts; they also will swoop to catch clams and other objects they have dropped before they hit the ground. This latter behaviour appears to be playful (as opposed to kleptoparasitic, for example) because: dropcatches were performed more by younger birds, dropcatches were not necessarily made over a hard substrate, the behaviour was sometimes performed with non-food objects, and it occurred more often during warm, windy weather (Gamble and Cristol, 2002).

There are good adaptive reasons for the existence of play, and scholarly discussions of play are usually in the context of its evolutionary benefit (Bekoff and Byers, 1998; Burghardt, 2005). Playing games of chase is no doubt beneficial for healthy, well-fed lambs, as it is for fox cubs, even though as adults these species may deploy these skills in different contexts (escape and pursuit, respectively). Yet, animals (including humans) do not consciously play for ultimate reasons; they play because it is fun to do so. Enhanced survival can be seen as a positive reward in the evolutionary sense, but not in the sense of experiencing a pleasurable sensation.

Thus, what is largely lacking in discussions of animal play is its affective element. Inasmuch as the context and expression of animal play often resemble that of human play, we may expect that it is pleasurable for them, too. Having fun seems to many of us the main characteristic of animal play (Burghardt, 2005). Burgdorf and Panksepp (2001) found that rats would run to the hand, on average, four times as quickly to receive tickles to their bellies (which mimic rats' rough-and-tumble play behaviour) than would rats trained to expect dorsal strokes. Several species are known to calibrate the boisterousness of their play, apparently to sustain the activity, which also suggests that they are enjoying it. Adult red-necked wallabies self-handicap against smaller and weaker playmates. For example, rarely does the larger partner rear up or kick; littler playmates are also much more vigorous in their play-fighting (Watson and Croft, 1996). Younger chimps are more likely to engage older chimps who are soliciting play if the latter shows self-handicapping behavior (Mendoza-Granados and Sommer, 1995). Young chimps (and other species) tested in the laboratory will choose play over food unless they are very hungry (Goodall and Bekoff, 2002), and there are anecdotal accounts of captive animals working for the chance to play (Linden, 1999).

We may say that the adaptive benefits of play are what sustains its expression in a gene pool, but if we are dealing with conscious, emotional animals, we can and should acknowledge the proximate role of pleasure (another product of evolution) in the interaction. This more inclusive interpretation is more thorough because pleasure acts as the proximate mechanism that causes animals (including humans) to behave adaptively—in this case, by playing.

## **Food**

Because food is so indispensable to an animal's survival, we may expect that conscious animals are highly motivated to obtain it, that they anticipate it, and that its consumption

brings rewards. We “know” (though the solipsist could challenge us) that humans have such a relationship to food. But the experience of food pleasure in animals is almost wholly unexamined.

There are innumerable clues that animals favour the flavour in their food. They show food preferences (e.g., Johnston and Fenton, 2001), tastes that change through time (Galef and Whiskin, 2003), and the anticipation of food (Tinklepaugh, 1928). Some, such as language-trained apes and parrots, can tell us their reactions to food (Barber, 1993; Linden, 2003). It has also been shown that animals produce pleasurable compounds known as opioids during both the search for food (the appetitive phase) and its consumption (the consummatory phase) (Berridge, 1996).

Facial responses to tastes are similar between rodents, primates and humans, suggesting shared evolutionary origins (Steiner et al., 2001; Cabanac, 2005). Enjoyably sweet flavours elicit characteristic licking responses, while aversive bitter tastes elicit gaping and head shaking. These behavioural responses are accompanied by activity in brain ‘hedonic hotspots,’ such as the nucleus accumbens and ventral pallidum, where neurotransmitters coordinate the “liking” of tastes (Pecin~a et al., 2006; Norgren et al., 2006). This linking of brain activity with positive patterns of behaviour (Berridge, 1996) suggests the conscious experience of pleasure.

A study of juvenile green iguanas showed that these animals would trade off the palatability of a bait (lettuce) with the disadvantage of having to venture into a very cold area to retrieve it. As the ambient temperature at the bait decreased, the lizards visited the bait less frequently and for shorter periods, choosing instead to stay under the heatlamp where nutritionally complete reptile chow was freely available. Moreover, time interval between sessions with bait (ranging from 1 to 8 days) had no effect on the duration of stay on the bait, suggesting that the lettuce was more of a luxury rather than an indispensable nutritional food source (Balaskó and Cabanac, 1998). Earlier experiments found that rats invariably shunned laboratory chow and ran into a cold environment to consume highly palatable foods, and that the animals’ individual preferences (which varied considerably) were reflected by the amount eaten, the number of excursions, and the time spent feeding in the cold (Cabanac and Johnson, 1983).

A compelling and ecologically important example of the hedonic aspects of food to animals is the evolution of fruit as a seed-dispersal mechanism. Fruit, to paraphrase botanist and science writer Michael Pollan, evolved as the product of a grand co-evolutionary bargain struck between plants and animals (Pollan, 2001). Desire, according to Pollan, is built into the very nature and purpose of fruit. He is correct, but you would have to search hard to find any scientists saying as much in a peer-reviewed journal. When I was researching this paper, I encountered a brief essay titled “Seed dispersal by animals: Behaviour matters,” by a then-doctoral student of botany at Washington State University. While lucid on the evolutionary facets of plant-animal coevolution, the writer nevertheless makes this characteristically agnostic statement:

*“Fruit appearance provides the cue for fruit choice, but nutrients provide the positive feedback that maintains an animal’s preference for the fruit.”(Yang, nd)*



Surely, if our own experience is any guide, what provides the animal with (immediate) positive feedback is not nutrients, but the taste of the fruit. Nutrients are the mediator; taste is the sentience pay-off. The more proximal experience of taste is an evolutionary product of what is nutritionally beneficial to the forager. And its flavour, not nutrient content directly, is what an animal experiences consciously when she selects and eats a fruit.

## **Sex**

It is hard to overestimate the importance of reproduction to an organism. Without it, species would cease to exist. Because reproduction is so important, natural selection should strongly favour behaviours that promote mate-seeking, mating and, where necessary, the raising of young. In conscious, feeling creatures, we may expect that what motivates them to behave in these ways is a combination of instinct on the one hand, and a powerful desire to attain reward on the other.

When it comes to sex, science is once again fixated on the ultimate, evolutionary context to explain how animals behave, and not the proximate, experiential context. Sexual activity in animals is conventionally portrayed as all business and no pleasure. The *Encyclopedia of Animal Behaviour*, for example (Bekoff, 2004), contains several entries about animal sexual behaviour, all of which interpret that behaviour solely in evolutionary contexts. From journal articles to textbooks to television documentaries, the idea that animals may be enjoying themselves is not explicitly rejected; it is not mentioned at all. The result is that there is precious little consideration of how animals might be feeling during sexual encounters, and how this, in turn, might affect their behaviour.

What, then, might be said of the role of pleasure in animals' sex lives? We do know that pleasure is a powerful reinforcer of sex drive in humans. Furthermore, the human quest for sexual gratification (and profit) manifests itself in an astonishing diversity (and, one might add, perversity) of sexual behaviour—witness a thriving pornography industry that caters to a wide range of individual sexual leanings and fetishes.

Against this human backdrop, sexual behaviour in nonhuman animals may appear both perfunctory and passionless, when it is observed at all. Yet, a good deal of animal sexual behaviour appears not devoted directly to the reproductive fitness (Bagemihl, 1999). In *Biological Exuberance: Animal Homosexuality and Natural Diversity*, Bagemihl surveyed of homosexuality and other forms of non-procreative sexual behaviour among mammals and birds. He found a lot of it.

And there is a lot of it. Many animals routinely copulate or engage in other sexual activities outside of the breeding season, including during pregnancy, menstruation (in mammals), and egg incubation. Such non-procreative activity may even constitute a large proportion of the animals' sexual behaviour, as it does, for instance, for common murrelets, proboscis monkeys, addax antelopes, rhesus macaques, wildebeest, golden lion tamarins, and mountain goats (see Bagemihl, 1999 for citations). Another variation on the theme of wasteful sex is group sexual activity wherein few if any participants are passing along genes. These sorts of orgies have been observed in spinner dolphins, gray and bowhead whales, swallows, and herons (ibid). Variations on non-copulatory mounting, include: mounts without erection, mounts with erection (but with no penetration), reverse mounting

in which a female mounts a male, mounting from the side or in positions from which penetration is impossible, which has been reported in mammals such as Japanese macaques, waterbuck, mountain sheep, takhi (Przewalski's horse), collared peccaries, warthogs and koalas, and birds including ruffs, hamerkops and chaffinches. Animals also engage in various forms of oral sex, stimulation of partner's genitals using the hands, paws, or flippers, and various forms of anal stimulation. There are also observations of interspecies sexual coupling in the wild (Bagemihl, 1999).

Skeptics might claim that these misguided antics are the fumbblings of young, confused or otherwise inexperienced individuals, though cases of oral or manual stimulation and cross-species interactions strain such claims. Behaviours that probably most suggest that sexual stimulation is pleasurable are various forms of auto-erotic behaviour. Owing to its utter futility for procreation, masturbation suggests that the performer merely seeks pleasure. Masturbation is widespread in mammals, and practiced about equally by both females and males (Bagemihl, 1999; Judson, 2003). It is known from at least seven mammalian orders, including primates, carnivores, bats, walruses, ungulates, cetaceans, and rodents. Masturbation appears less common in birds, but is not absent (e.g., Burger, 2001; Gaston and Kampp, 1994; Winterbottom et al., 2001).

Most biologists today recognize same-sex sexual interactions as being part of the normal, routine behavioural repertoire of the animals who engage in it. Currently, at least 300 species of vertebrates are known to practice homosexuality (Bagemihl, 1999). In most cases, participating individuals will also engage in heterosexual behaviour, and their sexual life history can most accurately be categorized as bisexual. Homosexual behaviour is clearly maladaptive from a strictly procreational standpoint, and while practitioners may benefit by gaining practice, or by releasing sexual tension, pleasurable rewards seem a likely motivation for engaging in it.

There are other bases for sexual pleasure in animals, including the prevalence of a clitoris in female mammals, and evidence for female orgasm in various primate groups, including apes, monkeys, lemurs and marmosets (Dixon, 1998; Bagemihl, 1999). In one study of Japanese macaques, female orgasmic responses were observed in 80 of 240 copulations (33%) (Troisi and Carosi, 1998).

## **Touch**

Unlike food or sex, touch is neither indispensable to survival nor to reproductive success. However, touch sensitivity is very useful. It allows animals to react adaptively to their environments. For example, being able to detect water movements helps fishes orient themselves in murky streams and on migration routes, and to detect the movements of other nearby animals, including potential predators. But for social species especially, touch often plays a key role in interactions with other individuals. Chimpanzees and other primates are well known for their proclivity to groom one another, which some species spend on average about 20% of their waking time doing (Uhlenbroek, 2002). Given its importance in these social contexts, we may expect that touch is a source of pleasure, as we know it to be from our own experience.

Very few investigators have addressed the pleasure of touch. In some cases, animals' liking of tactile contact may reveal itself by accident. For example, in a study in which dolphins could request rewards (pleasures) by pressing plastic symbols on a keyboard with the tips of their beaks, some animals favoured getting a rub to getting a fish (Linden, 2003). In some locations, whale-watchers have gained the trust of gray whales, who ride up against the sides of boats to have their bodies stroked and patted (Nollman, 1986). These examples do not prove that cetaceans enjoy the feeling of touch, but they are consistent with it.

There have been a few attempts to measure positive physiological responses in groomed animals. In primates, the release of pain-relieving endorphins has been demonstrated when they groom each other (Keverne, 1992). Evidence from horses supports a pleasant, calming effect. Like many other mammal species that form social groups, Camargue horses regularly engage in mutual grooming. When human researchers experimentally groomed them, the animals' heart rates dropped significantly, but only when the touch was directed at those areas of the neck that are the preferred grooming sites in this species (Feh and de Mazières, 1993).

As part of the study of tickling in rats mentioned earlier, tickled rats were trained for nine days to press a bar to receive tickling. A second, inactive bar elicited no tickling when pressed. On the test days that followed, the rats pressed the active bar repeatedly to receive tickling; they almost never pressed the inactive bar, and their bar-pressing increased during this period. For seven days of extinction testing, during which time bar-pressing elicited no tickling, use of the active bar declined significantly and by the fifth day was equivalent to presses on the inactive bar (Burgdorf and Panksepp, 2001).

Some interesting evidence for positive affect associated with touch has been documented in interspecies interactions in aquatic environments. At a freshwater spring in Kenya, fishes of various species gravitate to wallowing hippopotamuses, nibbling and plucking at their skin. Observations by biologists/photographers Mark Deeble and Victoria Stone indicate that the hippos are far from passive participants in these cleaning services. They deliberately splay their toes, spread their legs and hold their mouths open to provide easy access for the fishes, and they appear to solicit cleanings by visiting 'cleaning stations' where fish congregate (Deeble and Stone, 2001). The hippos were so relaxed during these "spa treatments" that they would sometimes fall asleep.

The widespread phenomenon of fish cleaning stations not only gives us a fascinating glimpse into the experiences of animals still assumed by many to have no feelings (Rose, 2007), they offer compelling evidence for the experience of tactile pleasure in fish. Cleaner fish of a variety of species nibble loose skin, fungal growths, and fish lice from other fish "clients." Wounds may also be plucked at, which may relieve infection and speed healing. It is a mutualism: cleaners benefit by getting food – delivered buffet-style by clients who line-up patiently to await their turn – and clients get a body-cleansing service. Different species of customers (or "hosts") are cleaned in a highly specific manner by cleaner fish (and shrimps), who advertise their services with brightly colored uniforms, and perform bobbing/fussing movements to signal their willingness to attend to clients. Clients also may signal their readiness, for instance by orienting themselves vertically in the water, and

opening their mouths and gills at appropriate times to allow access to the cleaner fishes (Potts, 1973).

There are features of the cleaner–client relationship that suggest positive feelings are involved. Invitation postures indicate that cleaners may be anticipating the attentions of clients, and clients the services of their hosts (Potts, 1973). Recent study of one of the principal cleaner species, the cleaner wrasse, supports the notion that tactile stimulation is an important motivator for the interaction. Based on 112 h of observation of 12 different cleaners, cleaners appear able to alter client decisions over how long to stay for an inspection, and to stop clients from fleeing or responding aggressively to a cleaner bite that made them jolt (Bshary and Wuerth, 2001). There is also evidence that cleaners and clients recognize each other (Tebbich et al., 2002), and that they return to their favoured business partner (Bshary and Shaeffer, 2002), much as we return to a favourite barber or hairdresser. Finally, cleaners sometime cheat by nipping off some of the client's own skin; established clients behave as if taking serious offense at this, chasing the cleaner around, and/or shunning the cleaner's future solicitations (Bshary and Grutter, 2005). This punishment helps to stabilize the relationship between cleaners and their clients.

### **Other pleasures**

Animals' lives afford them the opportunity to experience a wealth of other pleasures beyond the realms of food, sex and touch. Animals seek comfort, pursuing rewarding sensations that help maintain homeostasis (Cabanac, 1971), such as basking in the sun or seeking shade. Animals may also appreciate esthetic beauty; for example, female preference for showy male displays has driven sexual selection for elaborate beauty. And animals may experience a broad spectrum of emotions (Masson and McCarthy, 1995; Bekoff, 2007). Demonstrating these phenomena is challenging in species which cannot report their experiences in the way that humans can. As interest in the sensory experiences of animals rises, we may expect more ingenious methods to probe them, and more data to shed light on these topics.

### **PLEASURE'S MORAL SIGNIFICANCE**

What, if any, are the moral implications of animal pleasure? Does being not merely a pain-avoider but also a pleasure-seeker add to whatever moral implications may follow from the capacity for pain and distress? Beginning with 18th Century philosopher Jeremy Bentham's (1796) now famous appeal to animals' capacity to suffer ("The question is not: Can they talk, or Can they reason, but Can they suffer"), most of the recent scientific and philosophical discourse about animal welfare and rights has focused around pain and suffering. This is intriguing, for the consideration of pleasure has made some major contributions to moral philosophy. Utilitarianism, first expounded as a formal philosophy by Bentham, favours actions that optimize pleasurable outcomes while minimizing negative ones. Notably, Bentham regarded animals as serious objects of moral concern, based on their capacity for both pain and pleasure. That Bentham's utilitarianism has also been called Hedonistic Utilitarianism is a further acknowledgment of the importance of pleasures to considerations of right and wrong.

Peter Singer, the most influential contemporary utilitarian philosopher, has argued persuasively that sentient animals have interests, and that those interests involve not just avoiding physical pain and/or psychological suffering but also the experience of pleasure (Singer, 1975). But Singer himself admits to a general preoccupation with negative experiences: “. . .my focus has always been on animals’ capacity to suffer, from the time I started thinking seriously about the ethics of how we treat them” (Singer, 2007).

Some imbalance here is to be expected, given the greater urgency and gravity attached to pain and suffering when compared to pleasure. The avoidance of pain relates to matters of immediate survival; pain evolved as a means to avoid the greater penalty of death. Pain teaches individuals to avoid dangerous or harmful behaviours and encourages prudence in the decisions they make, for instance, in the pursuit of survival and social interactions. Pleasure, by comparison, does not normally hinge on the grave matter of survival, at least not in the immediate sense; obviously, if an animal were to ignore the motivations provided by the anticipation of food and the pleasure of its consumption, then that animal would soon die.

But the utter absence of any scholarly journal dedicated to positive feelings is surprising given pleasure’s important – arguably central – role in sentient experience. Readers might ask themselves what drew them to their career choice, and what motivates their preferences on a restaurant menu, their choice of clothing, or their weekend pastimes.

The capacity for good feelings has important corollaries for ethics. Lives that contain pleasure are lives with intrinsic value (Regan, 1983). That is to say, an individual who can experience good feelings has a life that is of value to that individual, independent of any value that individual’s life might have to another, for example as a source of entertainment, or revenue (ibid). Put another way, an animal who can experience pleasure has the capacity for a quality of life (McMillan, 2005). It is a life worth living, one in which there are better and worse days, and moments that are more or less pleasurable than others.

Humankind’s relationship to animals has been and continues to be one based mostly on a “might-makes-right” or “bright-makes-right” ethic. With our large brains and manipulative hands, our sophisticated language and technologies, we have evolved the capacity to control other animals completely. And we wield that control to the fullest. According to the Food and Agriculture Organization of the United Nations (FAO), over 50 billion land animals worldwide were killed for food in 2005 (Steinfeld et al., 2006). The numbers of individual fishes killed by humans are probably higher based on FAO statistics; global consumption in 2004 was 141.6 million metric tons (FAO, 2007). Close to 100 million animals are consumed yearly in laboratory experimentation in the United States (Carbone, 2004). The Humane Society of the United States estimates that each year over 50 million animals are killed for their fur (HSUS, 2007). Paradoxically, the number of animals we kill continues to rise, despite our greater appreciation for and ethical concern towards animals than ever before.

While there have been some scientific advances towards better understanding the animal’s experience of slaughter (Grandin, 1994; Gregory, 2004), modern methods of killing still involve intense levels of stress, pain and suffering (Warrick, 2001; Patterson, 2002; Scully, 2004). We may naturally conclude that harm is done to them. To the degree the victims can

also feel pleasure, it may not follow obviously that the harm of a painful, stressful end is amplified. Surely, it is suffering, not pleasure, that weighs on death.

Pleasure's moral significance resides in two aspects of our relationship to other animals. Each relates to the denial of pleasures. First, when we keep animals in impoverished conditions, as we do in factory farms, laboratory cages (Mason, 1991), and zoos (Jensen and Tweedy-Holmes, 2007), we deny them the opportunity to express natural behaviours. At least in rats and mice, studies show that animals bred for many generations in captive confinement retain behaviours of their wild ancestors (Estep et al., 1975; Boice, 1977), and that they are highly motivated to engage in behaviours that are a routine part of their day-to-day lives in nature, such as foraging, exploring, and social behaviour (Dawkins, 1988; Balcombe, 2006b).

One objection to this denial-of-pleasure argument is that captivity may offer the animal safe shelter from the vicissitudes of life in the wild (Tannenbaum, 2001). Wild existence can be hazardous, and some species may live longer in captivity (though others, such as cetaceans, do not). The problem with this objection is that a safer life is by no means a better life. We would be safer if we stayed home and never ate food prepared by others, for instance, but few of us would choose this mundane sort of existence. Another problem is that animals – like humans – prefer not to be confined; it is fairly axiomatic that animals prefer freedom to being in a cage.

The second form of denial of pleasure relates to death. In killing animals – especially young, healthy animals – we cause harm by denying them the opportunity to experience rewards that life would otherwise offer them. It may be claimed that a dead animal misses nothing. But the main reason that our criminal system treats murder so seriously is not that the victim may suffer—though that certainly compounds the crime. Murder is wrong because life, specifically that portion of life yet to be experienced, has value. Thus, killing is the greatest harm that can be done to conscious, autonomous beings (Balluch, 2006), and pleasure is firmly rooted in the harm committed.

## **CONCLUSION**

With the removal of former behaviourist taboos against subjective experiences in animals and the subsequent rise of cognitive ethology, there is an accelerating accumulation of information supporting animal sentience and awareness. Mice show empathy (Langford et al., 2006), sheep respond to the emotional states of other sheep (Da Costa et al., 2004), monkeys show a sense of justice (Brosnan and de Waal, 2003), starlings can become optimistic or pessimistic (Bateson and Matheson, 2007; Matheson et al., 2007), and rats show mirthful responses to tickling (Burgdorf and Panksepp, 2001). Science shows us that humans are not the only autonomous, sentient beings, or the only hedonists. Many other animals also have lives worth living. They do not speak as we do, but the scientific case that they have experiences is far stronger than the case that they do not.

The inevitable moral question arises: How can we reconcile our current treatment of animals with this knowledge? The answer, I believe, is that we decisively cannot. The reason for this lies in the principles that inform human law and policy. As autonomous, sentient beings, humans have intrinsic value. It follows that we have certain basic, inviolable rights

(provided we behave within the confines of the law), such as the right to freedom and the right to life. What grants us these rights is our intrinsic worth. Our reasoning and linguistic abilities are not the foundation of such rights, else we would deny them to the many humans who lack these capacities (Singer, 1975).

Despite this, our treatment of animals continues to languish in a Cartesian framework, one that permits the sacrificing of animals' most precious possessions (their freedom and their lives) for such relatively trivial human ends as gustatory pleasure, and recreation (Regan, 1983). Each hen in a battery house of 30,000 individuals has the capacity and potential to perform a range of highly motivated, rewarding behaviours, such as scratching, dustbathing and uttering and responding to a broad repertoire of social calls (Hughes and Channing, 1998; Widowski and Duncan, 2000; Evans and Evans, 1999). That she is unable to do so constitutes a denial of pleasures by human interference. Her suffering is compounded by the frustration of rewards. If we view animals' interests solely in terms of avoiding pain and suffering, then the case for their moral protection appears sound. When we include their capacity for pleasure, the case is made stronger.

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#### **REFERENCES**

- Bagemihl, Bruce, 1999. *Biological Exuberance: Animal Homosexuality and Natural Diversity*. Profile Books, Ltd., London.
- Balaskó, M., Cabanac, M., 1998. Behavior of juvenile lizards (*Iguana iguana*) in a conflict between temperature regulation and palatable food. *Brain, Behavior and Evolution* 52, 257–262.
- Balcombe, J.P., 2006a. *Pleasurable Kingdom: Animals and the Nature of Feeling Good*. Macmillan, London.
- Balcombe, J.P., 2006b. Laboratory environments and rodents' behavioural needs: a review. *Laboratory Animals* 40, 217–235.
- Balluch, M., 2006. Animals have a right to life. *ALTEX* 23, 281–286.
- Barber, Theodore X., 1993. *The Human Nature of Birds*. St. Martin's Press, New York.
- Bateson, M., Matheson, S.M., 2007. Removal of environmental enrichment induces 'pessimism' in captive European starlings (*Sturnus vulgaris*). *Animal Welfare* 16(S), 33–36.
- Bekoff, M. (Ed.), 2004. *Encyclopedia of Animal Behaviour*. Greenwood Press, Westport, Connecticut.
- Bekoff, M., 2007. Aquatic animals, cognitive ethology, and ethics: questions about sentience and other troubling issues that lurk in turbid water. *Diseases of Aquatic Organisms* 75, 87–98.

- Bekoff, M., Byers, J.A. (Eds.), 1998. *Animal Play: Evolutionary, Comparative, and Ecological perspectives*. Cambridge University Press, Cambridge.
- Bentham, J., 1789. *An Introduction to the Principles of Morals and Legislation*. T. Payne, London.
- Berridge, K.C., 1996. Food reward: brain substrates of wanting and liking. *Neuroscience and Biobehavioural Reviews* 20, 1–25.
- Beukema, J.J., 1970a. Angling experiments with carp (*Cyprinus carpio* L.). II. Decreased catchability through one trial learning. *Netherlands Journal of Zoology* 19, 81–92.
- Beukema, J.J., 1970b. Acquired hook avoidance in the pike *Esox lucius* L. fished with artificial and natural baits. *Journal of Fish Biology* 2, 155–160.
- Billings, J., Sherman, P.W., 1998. Antimicrobial functions of spices: why some like it hot. *The Quarterly Review of Biology* 73, 3–49.
- Boice, R., 1977. Burrows of wild and albino rats: Effects of domestication, outdoor raising, age, experience, and maternal state. *Journal of Comparative and Physiological Psychology* 91, 649–661.
- Brosnan, S.F., de Waal, F.B.M., 2003. Monkeys reject unequal pay. *Nature*, 425, 297–299.
- Braithwaite, V., 2007. In: *Do Fish Feel Pain?* . . . Proceedings of 21st IGN Meeting. Giessen, Germany, 20–21 September.
- Bshary, R., Grutter, A.S., 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters* 1, 396–399.
- Bshary, R., Shaeffer, D., 2002. Choosy reef fish select cleaner fish that provide high-quality service. *Animal Behaviour* 63, 557–564.
- Bshary, R., Wuerth, M., 2001. Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 268, 1495–1501.
- Budiansky, Stephen, 1998. *If a Lion could Talk: Animal Intelligence and the Evolution of Consciousness*. The Free Press, New York.
- Burgdorf, J., Panksepp, J., 2001. Tickling induces reward in adolescent rats. *Physiology and Behavior* 72, 167–173.
- Burgdorf, J., Panksepp, J., 2007. The neurobiology of positive emotions. *Neuroscience and Biobehavioural Reviews* 30, 173–187.
- Burger, Joanna, 2001. *The Parrot Who Owns Me: The Story of a Relationship*. Villard, New York.



- Burghardt, G.M., 1991. Cognitive ethology and critical anthropomorphism: a snake with two heads and hognose snakes that play dead. In: Ristau, C.A. (Ed.), *Cognitive Ethology: The Minds of Other Animals*. Erlbaum, San Francisco, pp. 53–90.
- Burghardt, G.M., 2005. *The Genesis of Animal Play: Testing the Limits*. MIT Press, Cambridge.
- Burghardt, G.M., 2007. Critical anthropomorphism, uncritical anthropocentrism, and naïve nominalism. *Comparative Cognition & Behaviour Reviews* 2, 136–138.
- Cabanac, M., 1971. Physiological role of pleasure. *Science* 173, 1103–1107.
- Cabanac, M., 2005. The experience of pleasure in animals. In: McMillan, F.D. (Ed.), *Mental Health and Well-being in Animals*. Iowa State University Press, Ames, pp. 29–46.
- Cabanac, M., Johnson, K.G., 1983. Analysis of a conflict between palatability and cold exposure in rats. *Physiology & Behavior* 31, 249–253.
- Carbone, L., 2004. *What Animals Want: Expertise and Advocacy in Laboratory Animal Welfare Policy*. Oxford University Press, Oxford.
- Colpaert, F.C., De Witte, P., Mondt, A.N., Awouters, F., Niemegeers, C.J.E., Jansen, P.A., 1980. Self-administration of the analgesic suprofen in arthritic rats: evidence of *Mycobacterium butyricum*-induced arthritis as an experimental model of chronic pain. *Life Sciences* 27, 921–928.
- Colpaert, F.C., Meert Th, De Witte, P., Schmitt, P., 1982. Further evidence validating adjuvant arthritis as an experimental model of chronic pain in the rats. *Life Sciences* 31, 67–75.
- Da Costa, A.P., Leigh, A.E., Man, M.-S., Kendrick, K.M., 2004. Face pictures reduce behavioural, autonomic, endocrine and neural indices of stress and fear in sheep. *Proceedings of the Royal Society Biology B* 271, 2077–2084.
- Danbury, T.C., Weeks, C.A., Chambers, J.P., Waterman-Pearson, A.E., Kestin, S.C., 2000. Self-selection of the analgesic drug, carprofen, by lame broiler chickens. *Veterinary Record* 146, 307–311.
- Dawkins, M.S., 1988. Behavioural deprivation: a central problem in animal welfare. *Applied Animal Behaviour Science* 20, 209–225.
- Dawkins, M.S., 1998. Evolution and animal welfare. *The Quarterly Review of Biology* 73, 305–328.
- Deeble, M., Stone, V., 2001. Kenya's Mzima Spring. *National Geographic* 200 (5), 32–47.
- Dehnhardt, G., Mauck, B., Hanke, W., Bleckmann, H., 2001. Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* 293, 29–31.

de Waal, F., 1991. Complementary methods and convergent evidence in the study of primate social cognition. *Behaviour* 118, 297–320.

Dixon, A.F., 1998. *Primate Sexuality: Comparative Studies of the Prosimians Monkeys, Apes, and Human Beings*. Oxford University Press, Oxford.

Ehrensing, R.H., Michell, G.F., Kastin, A.J., 1982. Similar antagonism of morphine analgesia by MIF-1 and naxolone in *Carassius auratus*. *Pharmacology, Biochemistry, and Behavior* 17, 757–761.

Elwood, R.W., 2007. In: *Pain and Stress in Crustaceans? . . . Proceedings of 21st IGN Meeting*. Giessen, Germany, 20–21 September.

Estep, D.W., Lanier, D.L., Dewsbury, D.A., 1975. Copulatory behaviour and nest building behaviour of wild house mice (*Mus musculus*). *Animal Learning and Behavior* 3, 329–336.

Evans, C.S., Evans, L., 1999. Chicken food calls are functionally referential. *Animal Behaviour* 58, 307–319.

Feh, C., de Mazières, J., 1993. Grooming at a preferred site reduces heart rate in horses. *Animal Behaviour* 46, 1191–1194.

Food & Agriculture Organization, 2007. *The State of World Fisheries and Aquaculture 2006*. FAO, Rome.

Galef Jr., B.G., Whiskin, E.E., 2003. Preference for novel flavors in adult Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology* 117, 96–100.

Gamble, J.R., Cristol, D.A., 2002. Drop-catch behaviour is play in herring gulls, *Larus argentatus*. *Animal Behaviour* 63, 339–345.

Gaston, T., Kampp, K., 1994. Thick-billed murre masturbating on grass clump. *Pacific Seabirds* 21, 30.

Grandin, T., 1994. Euthanasia and slaughter of livestock. *Journal of the American Veterinary Medical Association* 204, 1354–1360.

Gregory, N.G., 2004. *Physiology and Behaviour of Animal Suffering*. Blackwell Publishing, Oxford.

Goodall, J., Bekoff, M., 2002. *The Ten Trusts: What We Must do to Care for the Animals We Love*. HarperSanFrancisco, San Francisco.

Heyers, D., Manns, M., Luksch, H., Güntürkün, O., Mouritsen, H., 2007. A visual pathway links brain structures active during magnetic compass orientation in migratory birds. *PLoS ONE* 2, e937.

Hopkins, C.D., 1974. Electric communication in fish. *American Scientist* 62, 426–437.

Hughes, B.O., Channing, C.E., 1998. Effect of restricting access to litter trays on their use by caged laying hens. *Applied Animal Behaviour Science* 56, 37–45.

Humane Society of the United States, 2007. The Cruel Reality of Fur Production (cited 26 December 2007). Available from: [http://www.hsus.org/furfree/cruel\\_reality/](http://www.hsus.org/furfree/cruel_reality/).

Jensen, D., Tweedy-Holmes, K., 2007. Thought to Exist in the Wild: Emerging from the Nightmare of Zoos. No Voice Unheard, Santa Cruz.

Johnston, D.S., Fenton, M.B., 2001. The diets of pallid bats (*Antrozous pallidus*): variability at individual and population levels. *Journal of Mammalogy* 82, 362–373.

Judson, Olivia, 2003. Dr Tatiana's Sex Advice to All Creation: The Definitive Guide to the Evolutionary Biology of Sex. Vintage, London.

Kennedy, J.S., 1992. The New Anthropomorphism. Cambridge University Press, Cambridge.

Keverne, E.B., 1992. Primate social relationships their determinants and consequences. *Advances in the Study of Behaviour* 21, 1–36.

Langford, D.J., Cragger, S.E., Shehzad, Z., Smith, S.B., Sotocinal, S.G., Levenstadt, J.S., Chanda, M.L., Levitin, D.J., Mogil, J.S., 2006. Social modulation of pain as evidence for empathy in mice. *Science* 312, 1967–1970.

Linden, Eugene, 1999. The Parrot's Lament: And Other True Tales of Animal Intrigue, Intelligence, and Ingenuity. Dutton, New York.

Linden, Eugene, 2003. The Octopus and the Orangutan: New Tales of Animal Intrigue, Intelligence, and Ingenuity. Plume, London.

Macphail, E., 1998. The Evolution of Consciousness. Oxford University Press, Oxford.

Mason, G.J., 1991. Stereotypies and suffering. *Behavioural Processes* 25, 103–115.

Masson, J.M., McCarthy, S., 1995. When Elephants Weep: The Emotional Lives of Animals. Delacorte, New York.

Matheson, S.M., Asher, L., Bateson, M., 2007. Larger, enriched cages are associated with 'optimistic' response biases in captive European starlings (*Sturnus vulgaris*). *Applied Animal Behavior Science* 109, 374–383.

McMillan, F.D., 2005. The concept of quality of life in animals. In: McMillan, F.D. (Ed.), *Mental Health and Well-Being in Animals*. Blackwell Publishing, Ames, IO, pp. 183–200.

Mendoza-Granados, D., Sommer, V., 1995. Play in chimpanzees of the Arnhem Zoo: self-serving compromises. *Primates* 36, 57–68.

Nollman, Jim, 1986. Dolphin Dreamtime: Talking to the Animals. Anthony Blond, London.

Norgren, R., Hajnal, A., Mungarndee, S.S., 2006. Gustatory reward and the nucleus accumbens. *Physiology & Behavior* 89, 531–535.

Ortega, J.C., Bekoff, M., 1987. Avian play: comparative evolutionary and developmental trends. *Auk* 104, 338–341.

Patterson, C., 2002. *Eternal Treblinka: Our Treatment of Animals and the Holocaust*. Lantern, New York.

Panksepp, Jaak, 1998. *Affective Neuroscience*. Oxford University Press.

Peciña, S., Smith, K.S., Berridge, K.C., 2006. Hedonic hot spots in the brain. *The Neuroscientist* 12, 500–511.

Persinger, M.A., 2003. Rats' preferences for an analgesic compared to water: an alternative to "killing the rat so it does not suffer". *Perceptual and Motor Skills* 96, 674–680.

Pollan, Michael, 2001. *The Botany of Desire: A Plant's-eye View of the World*. Random House, NY.

Potts, Geoffrey W., 1973. The ethology of *Labroides dimidiatus* on Aldabra. *Animal Behaviour* 21, 250–291.

Regan, T., 1983. *The Case for Animal Rights*. University of California Press, Berkeley.

Rose, J.D., 2007. Anthropomorphism and 'mental welfare' of fishes. *Diseases of Aquatic Organisms* 75, 139–154.

Schulte-Pelkum, N., Wieskotten, S., Hanke, W., Dehnhardt, G., Mauck, B., 2007. Tracking of biogenic hydrodynamic trails in harbour seals (*Phoca vitulina*). *Journal of Experimental Biology* 210, 781–787.

Scully, M., 2004. *Dominion: The Power of Man, the Suffering of Animals, and the Call to Mercy*. St. Martin's Griffin, New York.

Singer, 1975. *Animal Liberation: A New Ethics for our Treatment of Animals*. Random House, New York.

Singer, P., 2007. Foreword to *Pleasurable Kingdom: Animals and the Nature of Feeling Good* (paperback edition). Macmillan, London, p. vi.

Steiner, J.E., Glaser, D., Hawilo, M.E., Berridge, K.C., 2001. Comparative expression of hedonic impact: affective reactions to taste by human infants and other primates. *Neuroscience & Biobehavioral Reviews* 25, 53–74.

Steinfeld, H., Gerber, P., Wassenaar, T., Castel, V., Rosales, M., de Haan, C., 2006. *Livestock's Long Shadow: Environmental Issues and Options*. FAO, Rome.

Tannenbaum, Jerrold, 2001. The paradigm shift toward animal happiness: what it is, why it is happening, and what it portends for medical research. In: Ellen, Frankel Paul, Jeffrey, Paul (Eds.), *Why Animal Experimentation Matters: The Use of Animals in Medical Research*. Transaction Publishers, New Brunswick, pp. 93–130.

Tebbich S, Bshary R, Grutter AS. Cleaner fish *Labroides dimidiatus* recognize familiar clients. *Animal Cognition* 5, 139–145.

Tinklepaugh, O.L., 1928. An experimental study of representative factors in monkeys. *Journal of Comparative Psychology* 8, 197–236.

Troisi, A., Carosi, M., 1998. Female orgasm rate increases with male dominance in Japanese macaques. *Animal Behaviour* 56, 1261–1266.

Uhlenbroek, Charlotte, 2002. *Talking with Animals*. Hodder & Stoughton, London.

Warrick, J., 2001. Modern meat: a brutal harvest. *The Washington Post* 10 (April), A1.

Watson, D.M., Croft, D.B., 1996. Age-related differences in playfighting strategies of captive male red-necked wallabies (*Macropus rufogriseus banksianus*). *Ethology* 102, 336–346.

Widowski, T.M., Duncan, I.J.H., 2000. Working for a dustbath: are hens increasing pleasure rather than reducing suffering? *Applied Animal Behaviour Science* 68, 39–53.

Winterbottom, M., Burke, T., Birkhead, T.R., 2001. The phalloid organ, orgasm and sperm competition in a polygynandrous bird: the redbilled buffalo weaver (*Bubalornis niger*). *Behavioral Ecology and Sociobiology* 50, 474–482.

Wynne, C., 2004. *Do Animals Think?* Princeton University Press, Princeton, NJ.

Yang, S., nd. Seed dispersal by animals: behaviour matters (cited 30 November 2007)

Available from:

[http://www.cnr.uidaho.edu/range556/Apl\\_BEHAVE/projects/seed\\_dispersal.html](http://www.cnr.uidaho.edu/range556/Apl_BEHAVE/projects/seed_dispersal.html).