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From an animal’s point of view:  
Motivation, fitness, and animal welfare

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Abstract: To study animal welfare empirically we need an objective basis for deciding when an animal is suffering. Suffering includes a wide range of unpleasant emotional states such as fear, boredom, pain, and hunger. Suffering has evolved as a mechanism for avoiding sources of danger and threats to fitness. Captive animals often suffer in situations in which they are prevented from doing something that they are highly motivated to do. The “price” an animal is prepared to pay to attain or to escape a situation is an index of how the animal “feels” about that situation. Withholding conditions or commodities for which an animal shows “inelastic demand” (i.e., for which it continues to work despite increasing costs) is very likely to cause suffering. In designing environments for animals in zoos, farms, and laboratories, priority should be given to features for which animals show inelastic demand. The care of animals can thereby be based on an objective, animal-centered assessment of their needs.

Keywords: animal care; animal welfare; behavioural ecology; consumer demand theory; emotion; ethics; experimental analysis of behaviour; mental states: motivation; operant conditioning

1. Introduction

Let us not mince words: Animal welfare involves the subjective feelings of animals. The growing concern for animals in laboratories, farms, and zoos is not just concern about their physical health, important though that is. Nor is it just to ensure that animals function properly, like well-maintained machines, desirable though that may be. Rather, it is a concern that some of the ways in which humans treat other animals cause mental suffering and that these animals may experience “pain,” “boredom,” “frustration,” “hunger,” and other unpleasant states perhaps not totally unlike those we experience.

This would appear to put scientists in a dilemma. If we insist that such subjective language has no place in science and that the mental states of nonhuman animals cannot be studied empirically, then we opt out of all debates about animal welfare, leaving the formulation of laws and regulations concerning the treatment of animals to those (often nonscientists) who may have no such scruples. On the other hand, if we feel that laws and regulations should be based on scientific knowledge about the animals (Dawkins 1980), we may feel we have a duty to step into these muddy waters and say what we can, even if we then risk being called unscientific. The purpose of this target article is to argue that we do not, in fact, have to choose between scientific respectability and practical considerations. A middle way is possible. We can acknowledge the genuine difficulty of ascertaining what a nonhuman animal feels and yet attempt to attain a scientific understanding of its feelings. Indeed, we should do so not only because we will thus promote the welfare of animals but because the study of subjective feelings is properly part of biology.

Some of this ground has already been broken by Griffin (1981). It has recently become permissible to talk about animals having “thoughts” or forming concepts (Terrace 1957; Walker 1953). What we need now is to come to grips with the wide range of unpleasant emotional states we call “suffering” (fear, loneliness, thirst) and the more pleasant ones we call contentment or well-being. The reason is that almost all arguments about the treatment of animals focus on the issue of suffering and the experience of pain. (See also Rachlin: “Pain and Behavior” BBS 811, 1985. [Singer (1976); see accompanying Precommentary], for example, argues that the capacity to suffer and to feel pain is central to the question of what is moral and what is not. He believes that this capacity is shared by humans and nonhuman animals and that consequently “speciesism” (discrimination against other species, Ryder 1975) is as reprehensible as sexism or racism. The idea that animals are morally the equals of humans and have “rights” comparable to those of humans is based on a belief in an equal capacity to suffer as well as on a belief that both have other similar attributes that influence subjective experience (Bollin 1981). Regan (1984, 1985) advocates the total abolition of the use of animals in research, commercial agriculture, and hunting for sport (see further discussions by Clark 1977; M. W. Fox 1986; Frey 1980; Midgley 1983).

Even those whose views are less extreme and who see humans as less important than nonhuman animals nevertheless think that animals deserve care and consideration. It is not essential to believe that animals have
rights comparable to those of humans to conclude that animals should not suffer unnecessarily (Cohen 1986, M. A. Fox 1986). Countries in many parts of the world have established, or are currently revising, legislation relating to the way animals should be treated in farms, zoos, and research institutions. Academic bodies have published guidelines for the use of animals in research (e.g., Animal Behavior Society/Association for the Study of Animal Behaviour 1986) and ethical issues regarding the use of animals have been openly debated in academic journals (Bowl 1980, Burghardt & Herzog 1980, Gallup & Suarez 1980, Huntingford 1984). Experiments on animals have recently been defended (Miller 1985, Paton 1984) and attacked (Sharpe 1987) with renewed vehemence. The moral basis of experimenting on animals is now being questioned and analyzed (Bateman 1986) and where possible, alternatives to the use of animals are being sought (Gallup & Suarez 1985).

None of this would be happening if many people did not believe that animals are in an important way different from inanimate objects such as national monuments or religious relics, entities that also receive protection. They are different because of their assumed capacity to feel, to experience subjectively. Many now agree that when an animal "suffers," its experiences unpleasant states and that they matter to it (Baxter 1983a; 1983b; Dawkins 1987; van Rooijen 1984; Zayan & Duncan 1985).

The growing interest in the ethical issues surrounding animal welfare thus forces us to consider the subjective feelings of animals and how we might best study them. Many attempts have already been made to define the signs of well-being and suffering in animals (Banks 1982; Barnett et al. 1985; Broom 1986; Brown 1981; Craig & Adams 1984; Dantzer et al. 1983; Duncan 1974; Ewbank 1985; Hill 1985; Kilgour 1985; McBride & Craig 1985; Morton & Griffiths 1985; Smidt 1983; van Putten 1981; Tschanz 1982), using the criteria of the animal’s physical health or changes in its physiology and behaviour. In this article I will concentrate on behavioural measures of ensuring welfare and will draw together work from applied ethology, psychology, and behavioural ecology. The aim throughout will be to attempt to understand how much of what happens to animals actually matters to the animals themselves. The animals’ point of view cannot be considered in isolation from long-term health interests (any more than a child’s view about going to the dentist can be). However, I shall argue that the animals’ viewpoint should be an essential ingredient in all animal welfare studies because it provides the only plausible bridge between observable events such as physiological and behavioural changes, which are the basic data at our disposal, and the subjective experiences of animals, which is the ultimate goal of animal welfare studies to understand.

2. “Suffering” and natural selection

In the rest of this paper “animal” will be assumed to mean nonhuman animals and “suffering” will refer to a wide range of unpleasant subjective states (e.g., boredom, frustration, thirst) that appear to have evolved by natural selection as means of avoiding danger or restoring physiological deficits resulting from animal’s natural environ-
For example, if a bird of a species that normally migrates in autumn is kept in a cage, it may be well cared for and its chances of surviving the winter may be considerably greater than those of its wild conspecifics that are free to migrate. But the caged bird’s behaviour has not evolved to meet this contingency. The bird is highly motivated to fly (as judged by its repeated attempts to escape); it is unable to do so, and may be “suffering” from its confinement. Wild birds of the same species may have little chance of surviving if they do not migrate, so the caged one is behaving “as if” death through failure to migrate were very likely. In other words, the canonical costs of not migrating may be very small, but the animal may suffer nevertheless.

The reason for this logical separation between canonical costs and suffering is that “canonical cost” refers to the ultimate or evolutionary effects of not performing a behaviour, whereas “suffering” is associated with the proximate or causal mechanisms underlying a behaviour. When animals are in their natural environments, proximate or causal mechanisms lead them to behave in ways that maximize fitness. But in unnatural environments, those same proximate or causal mechanisms may be activated irrespective of the consequences for fitness. If an animal’s assessment of a given situation is that it is in great danger if it cannot perform certain behaviours, then it will suffer even if it is not actually in danger.

In assessing whether an animal is suffering, therefore, we must take into account not just the canonical costs of preserving its fitness but the “perceived costs” — the costs as perceived by the animal (Dawkins 1988; cf. the “objective function” of McFarland & Houston 1981). Perceived costs are the proximate or causal counterparts of canonical costs. High perceived costs may or may not involve unpleasant subjective feelings. When they do have a subjective component, we call that state “suffering.” We must accordingly consider both the physical and psychological health of animals in assessing animal suffering and well-being.

Physical health requires that, at the very least, an animal be free from injury and disease, that is, that there be no obvious threats to its survival and reproduction. Physical health may also include the absence of less obvious physiological disturbances (Dantzler et al. 1983), and positive signs such as bright eyes and the ability to reproduce.

Psychological health is more difficult to identify but just as important (Dawkins 1980; Duncan 1974; Broom 1986; Kilgour 1983). As has just been suggested, an animal that is apparently in good health may experience suffering if the perceived costs of its confinement are high. Psychological health implies that perceived costs are low. In the next section I will consider how perceived costs can be measured and how they may be related to suffering.

3. Perceived costs and motivation

Thorpe (1965) and Martin (1975) argued that animals suffer when they are unable to perform the full repertoire of behaviours performed by members of the same species in nature. The reasoning if that an animal’s inability to perform any behaviour in its “natural” repertoire may entail a high perceived cost. This view has recently been endorsed by the U.K.’s Farm Animal Welfare Council (1986). Such a view is open to question, however. First, there may be major genetic or environmental differences between captive animals and the wild ones with which they are compared (Beilharz & Zeeb 1981; Price 1984; Wood-Gush 1975). Even feral animals (here meaning domesticated wild stock that have been allowed to run wild) may show genetic differences from the parent stock because selection can result in genetic changes in behaviour within a very small number of generations (Cade 1981, Majerus et al. 1982). Second, animals may acclimatise or adjust to their captive environments in their own lifetimes. An obvious example is the tameness of many zoo animals towards their keepers (Hediger 1964); this may be strikingly different from the behaviour of wild animals of the same species towards humans. The third and most important reason an animal may not suffer in captivity, even though its environment may be very different from that of a wild animal concerns the variety of control mechanisms underlying animal behavior. Domestic or zoo animals may not perform much antipredator behaviour if the critical stimuli are not present (see Ewert 1987). Out of sight may mean out of mind for captive animals, so the absence of a behaviour does not necessarily imply that they are suffering (Hughes 1980). Another possibility is that the environment in captivity may provide such good substitutes for its needs that the animal lacks the motivation to perform the behaviour normally found in the wild. Baxter and Robertson (submitted) studied the nest-building behaviour of pregnant sows and found that, if provided with straw, they would build nests like those built by wild or feral pigs and would perform an operant response to obtain straw. They also found, however, that if the sows were provided with large water beds, they displayed very little nest-building behaviour and did not perform the operant response, instead setting on the water beds to give birth. In this case, the end result of the natural behaviour of nest building (a comfortable nest seemed to be more important than the performance of the behaviour itself). Hence, sows may not suffer from being unable to build a nest as long as they have a comfortable place to farrow.

Herrnstein (1977) argues that it is not always the end result that matters; the actual performance of the behaviour may also be important (see also Hughes et al. 1989). Breland and Breland (1961) cite a number of cases where hungry animals decreased the rate at which they obtained food because they spent time performing “natural” behaviour that would be appropriate to obtaining food in the wild (e.g., “rooting” and digging by pigs). Inglis and Ferguson (1986) showed that starlings prefer to search for food rather than eat identical freely available food (also Carder & Berkowitz 1970; Neuringer 1969). Vestergaard (1980) has argued that the time course of dust bathing by hens is consistent with Lorenz’s model (1950, 1978) of accumulated motivational energy and that hens suffer if deprived of the opportunity to carry out this behaviour (Sambras 1982; Wenrich & Strauss 1977; but see Halliday 1983; Hinde 1970; Hughes 1980; Toates 1986, 1987).

What all this means is that whether an animal is highly motivated to perform a particular behaviour and whether it suffers as a result of not being able to do so are empirical.
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Questions. In the absence of any other evidence, we cannot assume that just because an animal has not performed a behaviour for a long time or cannot perform it within the physical confines of a small cage the perceived cost of not performing it is high. The likelihood of suffering from not performing a behaviour may differ among behaviours (Nicol 1987).

Studies of the behaviour of wild or feral animals (Duncan et al. 1975, McBride et al. 1969) are a starting point for the assessment of the welfare of captive animals because they provide a baseline against which behaviour in captivity can be compared (Dawkins 1989). For the reasons just given, however, we cannot assume that all differences between the behaviours of wild and captive animals are necessarily indicative of suffering. We need empirical evidence.

Two quite distinct problems arise in this kind of investigation. The first is to determine whether a relationship exists between strong motivation to perform a behaviour whose performance is prevented and the subjective feelings of the animal concerned. The second problem is the basic practical one of how to measure an animal’s motivation, particularly its motivation to do something it is prevented from doing. These two problems will be dealt with in turn in sections 4 and 5.

4. Motivation and subjective experiences

I have suggested that suffering may occur when captive animals are unable to do something they are highly motivated to do because it would normally reduce a risk to their fitness. But no clear relationship exists between motivation and subjective feelings of suffering.

Since subjective experiences are known only to the individual experiencing them, the only way we can infer their existence in any other being, human or nonhuman, is by analogy. Following J. S. Mill and what has become known as the “argument from analogy,” we know we have subjective feelings, we see we are very similar to another person; therefore, by analogy, we infer that the other person has subjective feelings similar to our own. Without such a leap, without this argument from analogy, we are locked within our own skins (Skinner 1963) condemned to a solipsistic view of the world, with ourselves as the only experiencers of anything subjective. Most of us unhesitatingly make such a leap with respect to other individuals. We have more doubts with regard to nonhuman animals because they are not similar to us, either in anatomy or in behaviour, and we may be uncertain whether the analogy is still valid. We need evidence that the similarity is sufficient to justify the analogy.

Cabanac (1979) has argued that the behaviour and physiological responses of humans and nonhuman animals to conditions such as water deprivation, cold, and fatigue are so similar that we are justified in making such an analogy. For example, both humans and rats show similar reductions in preference for sweet foods after food intake (Booth et al. 1972). Human subjects report that sweet tastes become less pleasant after a meal and then pleasant again as satiety fades (Ducalna et al. 1973). By analogy, Cabanac infers that rats experience pleasure or displeasure under similar circumstances. He notes that in both humans and animals, unpleasant subjective feelings (which in their extreme form we would call suffering, evolve as warning signs, signalling potential harm to the organism.

It is important to point out that in assuming that humans and animals are similar in their capacity to experience suffering we make only minimal use of the argument from analogy. We do not need to assume that animals experience things exactly the way humans do or that they suffer in the same situations. But if we had prior evidence that an animal had strong motivation to escape from or to obtain something and was prevented from doing so we could assume that this condition was accompanied by an unpleasant experience, as it would be in the case of a human being. Animals may be completely different from us in their likes, their dislikes, and in what they attempt to escape from (Nagel 1974). But if we assume that they are like us in just one important respect (namely, that they too have unpleasant subjective experiences when they are prevented from doing things they are strongly motivated to do), we have a bridge between our subjective world and theirs. We can then leave it to empirical investigation to determine what animals will strive to obtain or to avoid and thereby derive an animal-based view of when they suffer. What we need are reliable methods of measuring animal motivation.

5. Indicators of high motivation

Ethologists and psychologists have adopted a variety of approaches to the problem of how to measure an animal’s motivation to perform a behaviour. One line of argument among applied ethologists has been that the tendency to perform behaviour in the absence of suitable stimuli is an indication of strong motivation (Black & Hughes 1974; van Putten & Dammers 1976). For example, hens in battery cages go through all the motions of dust bathing on bare wire floors even though there is no dust or litter. Ethologists have interpreted such “vacuum activities” as indicators of high levels of motivation (Vestergaard 1980), a view that owes much to Lorenz’s (1950, 1975) psychohydraulic model. (See also Ewert. “Neuroethology in Toads” BBS 10:3 1987) One of the complications in interpreting these activities as signs of suffering is that their performance may itself reduce the motivation to perform the behaviour (Heiligenberg 1965).

A related finding is that animals prevented from performing certain kinds of behaviour may show a greatly increased tendency to perform that behaviour when eventually given the chance: the “rebound effect” (Nicol 1987; Sambraus 1982; Vestergaard 1980; Wennrich and Strauss 1977). One possible explanation for such an effect is that the animals are merely responding to the novelty of the opportunity presented to them: however, the high levels of response in some cases do indeed seem to result from rising motivation during the period of deprivation (Metz 1955; Nicol 1987; Vestergaard 1980).

A third and very important motivational finding is the display of novel or “abnormal” behaviour, a large and miscellaneous category including displacement activities and stereotypes (fixed behavioural sequences performed repetitively and with no obvious function). For example, an animal that is prevented from reaching its food or does not find water where it has learned to expect it may
exhibit a range of behaviours apparently unrelated to feeding or drinking such as pacing, aggression, or grooming (Roper 1984). Such "displacement activities" of animals on intensive farms or in zoos have been used as evidence of strong motivation to do something that cannot normally be done in those environments (Duncan 1970). The same interpretation has been made of stereotypes (Broom 1983; Wiepkena et al. 1983). The causal basis of stereotypes is still unclear (Broom 1983; Danzger 1986), although they are often associated with food deprivation (Appleby & Lawrence 1987; Rushen 1985) and may also be part of an animal's means of coping with a restricted environment through the release of endorphins (Dantzger & Mormede 1983).

Psychologists too have long tried to measure the strength of an animal's motivation. Warden et al. (1935) list a number of possible measures, including how quickly an animal learns a task or how much electric shock it will tolerate to obtain a reward. Warden himself was aware of the problems with these methods - for example, that speed of learning will confound learning ability with motivation and that the shock method is very unreliable. His rats often refused to do anything if shocked. Other measures of motivation include the rate of consumption e.g., the rate of ingesting water as an indicator of drinking motivation (Stellar & Hill 1952), speed of running down an alley towards a reward (Cabanac & Johnson 1983), and the amount of time spent consuming food or water (Lester 1984; Silby & McFarland 1976). As Miller (1956) pointed out, however, these different ways of measuring motivation may yield different results. Moreover, the observed behaviour may be the net result of the contribution of a number of different subsystems affected in different ways (Teitelbaum 1982). Feeding behaviour, for example, is affected by the dietary content of the food, the presence or absence of predators (Milinski & Heiler 1978), the presence of conspecifics, and many other factors.

Cabanac (1985) used a modified version of Warden's (1931) obstruction method to measure motivation. In Warden's experiments, a rat could reach a reward (food, water, a female for a male, her pups for a female) only by walking over an electrified grid, but the rat was removed as soon as it touched the reward. Cabanac, using the food reward in a more natural setup, made his rats leave their warm nest and forage at 15°C but allowed them to eat once they reached the food. Their motivation for feeding was thus measured by the extent to which they were prepared to overcome the obstacle of cold following different durations of food deprivation. Cabanac found that the rate of eating and meal durations were not influenced by food deprivation, whereas the amount of food consumed, the number of meals eaten, and the speed of running to the feeder were.

Of the various methods of measuring animal motivation, those used by ethologists tend to focus on the animal's response when there is no opportunity to carry out a particular behaviour (e.g., vacuum activities, displacement activities, and stereotypes). Unfortunately, there is still much we do not understand about why animals make these responses and the effects of performing them. Some investigators have asserted (without supplying evidence) that if animals perform stereotypes for long periods (e.g., more than 10% of their waking lives), then they are suffering (Broom 1983; McBride & Craig 1985; Wiepkena et al. 1983). The shortcoming of the ethological methods is that no one has established how much the deprivation that gives rise to the abnormal behaviour matters to the animals themselves. We do not know how much vacuum activity or stereotyped behaviour indicates motivation strong enough to warrant being called suffering.

The methods used by psychologists have tended to concentrate on the behaviour that occurs after the deprivation period is over or on the animal's attempts to obtain a commodity (food, water) by paying a price such as having to press a bar or to tolerate cold or an electric shock. An animal's willingness to pay a price suggests that we can make a link between what an animal does and what it is feeling. As Cabanac (1985) puts it, "What is measured is not a motor response but rather the decision made by the subject to overcome a resistance to obtain a reward."

Recently, measurements of the price animals are willing to pay have been interpreted in terms of an economic framework that seems particularly useful for the study of animal welfare.

3. The economics of choice

Both biologists (McFarland & Houston 1981; Rapport & Turner 1977; Stephens & Krebs 1986) and psychologists (Lea 1978; Rachlin et al. 1981; Staddon 1980) have applied economic concepts to the study of animal behaviour. In this section it will be argued that, on the basis of data on what animals do when allowed to make a choice, we can infer perceived costs with the help of such economic concepts. (For a full description of the analogy between economics and ethology, see McFarland & Houston 1981.)

An animal's preferences for certain foods and temperatures, numbers of social companions give a first indication of its view of the world. Preferences can be measured either directly by providing an animal with an array of options and seeing which one(s) it chooses (the choice test), or indirectly by requiring the animal to make some response such as pressing a lever or pecking a key to produce or to avoid certain consequences (operant conditioning). Both methods have now been used extensively to study the responses of farm animals to different sorts of flooring (Hughes 1976; Hughes & Black 1973; Irps 1983; Ponteaux et al. 1983; van Rooijen 1985), different-size cages (Dawkins 1981; Faure 1986; Lagadic & Faure 1987; Nicol 1986), the vibration and noise of a transport vehicle (Bailey et al. 1983), different temperatures and light levels (Baldwin & Start 1985; Curtis 1983; Morrison & McMillan 1985; Richards 1976), and many other factors (Bellharz & Zeeb 1981; Kilgour 1976; Matthews & Temple 1979; Temple & Foster 1980).

Once the preferences and operant rewards have been established, it is possible to determine how much value the animal places on them by making it pay a (perceived) price, for example, having to peck a key or press a lever many times to obtain the same reward.

If an animal's preference is still apparent when it has to work harder (e.g., when it must perform a larger number of bar presses for the same amount of reward), the animal is said to exhibit "compensation" (Hogan & Roper 1978)
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or "resilience" (McFarland & Houston 1981). To use the terminology that psychologists have borrowed from economics, the animal's behavior reflects "inelastic demand" (Hrusa 1984; Lea 1978; Staddon 1980). In economics, price elasticity is the ratio of the percentage change in consumption to the percentage change in price. It is calculated by holding everything else — income and prices of other commodities — constant, and varying the price of the commodity in question. Commodities for which a given percentage increase in price results in a small change in the quantity demanded are called "inelastic demand" and are sometimes called luxuries; those for which a given percentage increase in price results in a large change in the quantity demanded are said to have an "elastic demand" and may be called necessities. There is clearly a continuum between elastic and inelastic demand, but economists use a slope of −1 as the boundary. (An alternative is to measure income elasticity: the percentage change in demand in response to a given change in "income," or the total time available to the animal for performing its entire behavioral repertoire.) Elasticity of demand is a key concept for the study of animal welfare (Dawkins 1983) because it shows how important different environments or commodities are to the animals themselves.

When food is the reward, animals usually appear to be prepared to work harder for the same amount of reward (Collier et al. 1972; 1986; Hogan et al. 1970; Hrusa 1984; Marwine & Collier 1979); in other words, their behavior indicates an inelastic demand. With other rewards, or with activities other than eating, demand is often elastic: The animal's preference is apparent when the cost of obtaining the reward is low but not when the animal must work hard for it. Elastic demand has been reflected in behaviors performed to gain access to a rival (Hogan et al. 1970; Thompson 1964) and to obtain light (Findley 1959).

Demand functions have been used to assess the relative value of a range of stimuli to farm animals. For example, Matthews and Ladewig (1987) used an operant procedure to present pigs with food, social contact with a familiar pig, or an empty chamber. Price increases for each reinforcer were stimulated by increasing the fixed ratio of reinforcement in sequence 1, 2, 5, 10, 15, 20, 30. The demand for social companions was found to be more elastic than that for food. Other methods that have been used to increase price include (1) increasing the weight of a door that a cockerel must push to obtain access to a female or to another cock (Duncan & Hughes 1988) and (2) increasing the wind speed that hens must tolerate to obtain litter (Lagadic & Faure, in preparation). Laying hens push heavy weights to gain access to nest boxes and continue to do so when the weights are increased, thus indicating inelastic demand (Duncan & Kite 1987).

There are several problems in interpreting demand curves, however, particularly when operant conditioning is used. It may be difficult to train animals to make operant responses to obtain certain kinds of rewards (Dawkins & Beardsley 1986; Hogan & Roper 1978; Roper 1983; Sevener 1973; Shettleworth 1973). This may seriously confound the comparison of demand curves corresponding to different behaviors, since a steeply sloping demand curve, suggesting elasticity of demand, may in fact reflect incompatibility of response and reinforcer and not necessarily low motivation. Animals may also be more prepared to work for a reward if they can see it (Dawkins & Beardsley 1986; Duncan & Hughes 1988).

A second difficulty is that short-term choices made in response to an immediate need may not reflect the animal's long-term preference. Hens that are about to lay have such a strong preference for nests that they will enter trammels even when the consequence is that they will have no food or water for the next 24 hours (Duncan 1978). If tested just before laying, they choose the nest, if tested just after laying, they choose food and water. Animals generally have a preference for immediate rather than long-term rewards (Timberlake 1984). [See also Logue: "Research on Self-Control" BBS 11(4) 1988.]

The first problem — the possible incompatibility between response and reinforcer — can be overcome by measuring demand curves based on data from several tests other than bar pressing and key pecking and by attempting to elicit responses that are more closely related to the kind of behavior the animal might perform in the wild. The second problem — the time scale over which preferences are measured — can be overcome by giving an animal the opportunity to change its behavior continuously over long periods. For example, instead of being given a brief opportunity once a day to perform an operant response, the animal can remain for long periods in a cage in which pressing different levers gives it access to food, water, and exercise (Collier et al. 1972). A joint consideration of these two problems suggests that a particularly fruitful research strategy might be to examine the way animals allocate their time over long periods and to stimulate the price they would have to pay if in their natural environments.

Survival and reproduction depend on whether an animal allocates the right amount of time to different behaviors and performs the behaviors at appropriate times of day, as determined by such factors as food reserves (Metcalfe & Furness 1984), risk of predation (Barnard 1980; Caraco et al. 1980), available time, and results of behavior earlier in the day (Houston & McNamara 1982, 1985; Katz 1974; Mangel & Clark 1990). Even the fact that many wild animals spend a large proportion of the active part of the day resting and apparently doing nothing (Herbers 1981; Sutherland & Moss 1985) can be regarded as an adaptive strategy, since periods of inactivity may be essential for digestion (Behrends 1981; Diamond et al. 1985), energy conservation (Anderson & Harwood 1985), or avoiding predators.

Animals adjust their time budgets according to the costs of the various activities. Müller-Schwarze et al. (1984) experimentally reduced the milk supply of white-tailed deer fawns and found that they increased their grazing by 62% and achieved a virtually total energy compensation, even though they had to curtail their other activities to do so. Johnson and Cabanac (1982a) studied rats in an environment that included a warm nest box and food in a cold area some distance away. They increased the cost of obtaining food by altering the air temperature (25°C, 5°C, or −15°C). The rats were able to maintain a near-normal balance of food intake and body temperature by reallocating the time spent feeding and sheltering and by changing their eating speed. When Johnson and Cabanac (1982b) kept the temperature of the feeding area constant at −15°C and varied the cost of obtaining food by varying the distance from food to the refuge (1, 2, 4, 8, or
16m), the rats maintained the same rate of eating and their total feeding time remained constant but their skin
and core temperatures dropped. The demand for food
remained the same despite the real cost in terms of body
warmth.

Hill et al. (1986) used a time budget manipulation with
growing chicks, but instead of changing the cost of one
commodity, they altered the total light period and there
fore the length of time available for any activity normally
performed in the light (the equivalent of income:
McFarland & Houston 1981). When light periods were
short, a given amount of time spent feeding was costlier in
terms of the time left over for other activities than when
light periods were longer. Nevertheless, the chicks con

continued to eat the same amount, changing their rate of
feeding rather than eliminating other activities. Dunbar
and Dunbar (1986) studied the time budget changes that
are made naturally by gelada baboons as the infants grow
older. The time the mothers spent feeding increased, but
the time devoted to social activities seemed to reflect
inelastic demand. Baboons found time to socialise, even
when they had to spend a great deal of time feeding, by
taking time away from resting.

Laying hens show a preference for being with social
companions even when the cost is increased by placing
physical barriers in their way, thus reflecting elastic
demand (Bubier, in preparation). Under the same condi
tions, the behaviour of hens reveals an inelastic demand
for food, and also for the opportunity to peck and to scratch in
litter, Dawkins, in preparation; Lagadic & Faure, in
preparation). Even when food is freely available else
where, hens will pay a price to be able to carry out the
"natural" feeding behaviour (Dawkins 1989).

7. Demand curves and suffering

By experimentally manipulating costs we can obtain a
rank order of the importance of different commodities or
activities based on the relative slopes of the demand
curves. Suffering is most likely to occur if animals are
prevented from performing the activities or deprived of
the commodities whose demand curves have the flattest
slopes (inelastic demand). Note that this measure is not
the same as the absolute frequency with which the animal
performs the behaviour under natural conditions, the
parameter that Thorpe (1967) suggested as the indicator
of what is essential to the animal. The demand curve for
behaviour that occurs rarely but is still performed when
costs are imposed would have a flat slope (inelastic
demand); the curve for commonly occurring behaviour that
disappears in the presence of imposed costs has a steep
slope (elastic demand).

How inelastic must demand be to indicate suffering?
Since food is essential to survival, and prolonged depriva
tion leads to clinical symptoms of ill health, a comparison
between the slopes of the demand curves for eating and
for other activities can be used as a welfare yardstick.
Commodities with demand curves similar to that of food
can be regarded as essential to welfare. From the animal's
point of view, they are as important as food and should
have top priority in the design of animal housing.

Several different sorts of evidence (physiology, health,
and the animal's willingness to work) all point to the
conclusion that hens suffer in the restricted space of many
cages. Demand curves (indicating the animal's point of
view, or perceived costs) often confirm evidence from
other measures of suffering. Caged laying hens will peck
a key to obtain more space than they are generally given in
battery cages (Lagadic & Faure 1988). The most recent
European Economic Community recommendation is 450
sq cm per bird and many birds in Europe and elsewhere
are given even less space than that. There is also evidence
that plasma-corticosteroid levels are highest at highest
bird densities (Cunningham et al. 1987) and that brittle
bones, leading to a high risk of breakage, are characte
ristic of birds kept in crowded conditions (Wabek &
Merkley 1974). As argued earlier, perceived costs are
particularly important in welfare studies, for they are as
close as we are likely to come to an accurate estimate of
the animal's own subjective view of the situation. They
may also indicate the existence of other conditions that
cause suffering but that may not be revealed by other
methods; for example, the importance of nesting mat
erials, substrates to forage in, objects to manipulate. There
may be situations in which physiological or health criteria
have not yet been determined, are difficult to interpret,
or become evident only after a long time.

8. Aversion

Thus far, we have considered the subjective feelings that
animals may have when deprived of conditions they will
work hard to obtain if given the opportunity (depriv
ation). It is also important to consider the possible suffer
ing caused to animals kept in conditions that they will
work hard to escape from (aversion).

The indexes of acute pain have been considered by, for
example, Chapman et al. (1985), Kitchell and Erickson
(1983), Melzack and Wall (1983), Morton and Griffiths
(1985), and Sanford et al. (1986). Following Russell and
Burch (1959), Rushen (1986b) has recently reviewed the
ways in which aversion learning can be used to establish
whether handling procedures, veterinary treatments,
and transport cause suffering to the animals subjected to
them. He makes the assumption that electrical shocks
cause suffering (pain) to nonhuman animals just as they do
to humans and that shocks of high intensity or long
duration are more painful (make the animal feel worse)
than shocks of low intensity or short duration. He then
argues that an animal's response to electrical shock can be
"titrated" against the animal's response to some other
variable such as the way it is handled.

Rushen (1986b) reports an experiment titrating elec
tro-immobilisation against physical restraint for sheep
running through a shearing area. In Australia, an electric
current is sometimes passed through sheep's bodies to
keep them from moving while they are being sheared.
Sheep that have been immobilised in this way are more
reluctant to run over the same ground on subsequent
occasions than sheep that have been physically restrained
in a sheep-handling machine, suggesting that elec
tro-immobilisation is more aversive (is more of a punish
ment) than physical restraint. The "conditioned suppres
sion" of a previously learned response such as bar pressing
can also be used to test unpleasantness. An animal first learns
that pressing a bar delivers food; then it learns that when a

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light comes on it will get an electric shock if it presses the bar (Blackman, 1977). The extent to which bar pressing is suppressed when the light appears indicates how unpleasant an experience the shock is for the animal (Baldwin & Stephens 1973; Dantzer & Baldwin 1974). Animals appear to be sensitive to the cost of such a suppression, since the degree of suppression that occurs in a given experiment is reduced by periods of food deprivation. When food is worth more to the animal, suppression is increased by partial satiation (Millenson & de Villiers 1972). Individual animals may vary in how aversive they find a given level of shock, so the degree of shock can be varied to give the same degree of punishment using individually calibrated degrees of response suppression (Rawlins et al. 1980). The degree to which the punishing effects of shock are alleviated has been used as a practical indicator of the intensification of unpleasant emotional states by certain drugs (Gray 1977). This is a clear example of reliance on the presumed relationship between punishment and suffering.

As in the case of deprivation we need a yardstick to relate the cost the animal is prepared to bear to avoid x to the suffering caused by being forced to remain in the presence of x. Titration against different degrees of food deprivation may be one solution. An animal that is prepared to forego a given amount of food (deprivation of which is known to cause weight loss and deterioration of physical condition) to avoid a particular treatment would most likely suffer if it were forced to undergo that treatment. This assumption can be used to answer some of the most important questions concerning animal welfare, such as whether pre-slaughter stunning is painful (Leach et al. 1980), and how much animals suffer from the various experimental procedures they are subjected to in laboratories.

9. Problems with the aversion learning approach

Although data on the price an animal is prepared to pay to gain access to or escape from something are the most direct measures we have of what that animal may be experiencing, there are several problems with this approach that must be confronted if the results are to be interpreted correctly.

1. The nature of the price paid may affect the slope of demand curves (section 6). In particular, incompatibility of reinforcer and response may give a false impression of low motivation. The solution to this problem is to plot and compare the demand curves and to increase the price in several different ways to make sure the apparent elasticity (or inelasticity) of demand is real.

2. The suppression of operant responses by stimuli that predict shock may vary depending on whether the paradigm used is a "conditioned emotional response" (shock delivered regardless of the animal's behavior) or a "discriminated punishment" (shock delivered only if an operant response is made; Rawlins et al. 1980). This variation must be investigated so the most appropriate procedure can be chosen (Rushen 1966a; also section 8).

3. The price an animal is prepared to pay may depend on the availability of substitutes. The price that rats are prepared to pay for food depends on whether sucrose is present (Lea & Roper 1977). Availability of substitutes is a factor, but not a major problem in welfare work. If an animal is demonstrably not willing to work hard for something because acceptable substitutes are available, it is probably not suffering according to the criteria developed in this paper.

4. The slopes of demand curves may depend on whether the experiment is set up as an "open economy" or a "closed economy" (Houston & McNamara 1955; Hursh 1954). If the animal is put into the experimental situation for just a short period each day and gets most of its food and exercise outside the experimental environment (open economy), its motivation to perform one behaviour rather than another may be quite different from its motivation when it lives in the experimental environment (closed economy) and has complete control over what it does throughout the day. For various reasons (Houston & McNamara, unpublished), long-term, closed economy experiments are more likely to produce valid results.

5. The animal may not be able to plan far enough ahead to make the right decisions for the whole day (Duncan 1975, Kagel et al. 1986; Timberlake 1984), possibly because of the unnaturalness of some experimental situations. As in (4), long-term experiments in which the animal is observed for long periods are most likely to yield valid results.

6. The price an animal is prepared to pay for something may depend on the predictability of the environment. A perceived risk that food may not be available in the future may render the present food source more attractive (Caraco et al. 1960; Stephens 1981). Again, this is not a serious problem. It simply means that the effect of predictability (or the lack of it) should be investigated.

7. What the animal chooses to pay for may not be beneficial to its physical health in the long run, as pointed out by Duncan (1978) and van Rooijen (1984). As emphasized in section 5, the solution is to take into account more than one measure of welfare (Dawkins 1980; Duncan 1974; Kilgour 1965).

8. There may be some states of suffering in which an animal cannot be said to be motivated to do anything at all. For example, it might have a tumour that causes it to be inactive. Animals' physical and psychological health must always be the first criterion of their welfare demand curve analysis should recognize its effect on motivation.

9. Demand curves may be nonlinear. An animal's behavior may seem to indicate elastic demand for some commodity when the cost is first increased, or the animal may drastically reduce the time it allocates to a particular behaviour, when the total time available is reduced. As the price is increased still further, however, the animal may still "insist" on paying the price to perform the behaviour for a short time each day. The only solution is to make sure that the range of price changes is sufficient to determine the true slope of the demand curve.

None of these problems is insoluble; all should be carefully considered in the design of any experiment. They do not detract from the usefulness of demand curve analysis or aversion learning as methods that describe as accurately as possible the animal's subjective experiences.
10. Conclusions

1. A central problem in the study of animal welfare is to define situations in which animals ‘suffer’ (experience a range of unpleasant subjective states, such as hunger, fear, and pain).

2. Suffering occurs when otherwise healthy animals are kept in situations that they will pay a high price to escape from (aversion) or in situations that, because they are being deprived of certain stimuli or behavioural possibilities, they will pay a high price to obtain (deprivation).

3. High cost is shown graphically by a demand curve with a flat slope (inelastic demand), which indicates that the commodity in question is important to the animal. If the slope of a commodity’s demand curve is similar to that of the demand curve for food, we can conclude that being deprived of that commodity matters to the animal as much as does food deprivation.

4. Demand curves can be constructed to show (a) changes in “income,” and (b) changes in the cost of performing individual behaviours. The latter demand curve can be most conveniently plotted by altering the schedules of reinforcement in an operant conditioning experiment; but because of the potential problems raised by using this approach for some kinds of behaviour, time budget manipulations in more natural environments may yield better results.

5. In designing environments for animals in zoos, farms, and laboratories, priority should be given to providing commodities and behavioural opportunities for which the animals’ behavior reflects inelastic demand.

Precommentary

The significance of animal suffering

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Nonhuman animals can suffer. To deny this, one must now refute not just the common sense of dog owners but the increasing body of empirical evidence, both physiological and behavioral (Dawkins 1980; Rollin 1989). My inquiry in this precommentary takes the existence of animal suffering for granted. The question is: Does the suffering of nonhuman animals matter? If so, how much does it matter? When it comes to a choice between human welfare and the suffering of nonhuman animals, how should we choose?

Many people accept the following moral principles:

1. All humans are equal in moral status.
2. All humans are of superior moral status to nonhuman animals.

On the basis of these principles, it is commonly held that we should put human welfare ahead of the suffering of nonhuman animals; this assumption is reflected in our treatment of animals in many areas, including farming, hunting, experimentation, and entertainment. I shall argue the contrary: that the combination of the two principles cannot be defended within the terms of any convincing nonreligious approach to ethics. As a result, there is no rational ethical justification for always putting human suffering ahead of that of nonhuman animals.

Before I defend this claim, a word about religious ethics. It is of course no accident that the principle of human equality and the principle of animal inferiority are widely held in Western society. They reflect a Judeo-Christian view of the human-animal relationship. Genesis tells us that God gave human beings dominion over the beasts. This has generally been interpreted to mean that we human beings have divine warrant for always giving priority to human interests. A clear example can be seen in the work of William Paley, a progressive moral theologian of the late eighteenth century. He wrote that the practice of killing animals to eat them caused them pain and death for our pleasure and convenience; moreover, eating meat was unnecessary, since we could live on fruits and vegetables, as the Hindus do. We are therefore “obeholden for it to the permission recorded in Scripture . . . .” (Paley 1785). It is true that some Christians have argued for a very different interpretation of the Christian tradition, one much more favorable to nonhuman animals (Attfield 1983; Linzey 1987). But I am putting aside such theological questions, partly because there is no rational foundation for the premises on which they are based, and also because if we are considering public policy in a pluralistic society, we should not take a particular religious outlook as the basis for our laws.

Let us examine the two principles just stated. If they are to be held in combination, we can expect that there is some characteristic possessed by all human beings, but not possessed by any nonhuman animals, by virtue of which all human beings are equal, and nonhuman animals are less than equal to humans. But what might that characteristic be?

One possible answer to this question is that the characteristic is simply that of being human. But this merely invites a further question: Why does “being human” matter morally? Here we can go in either of two directions, depending on how we understand the term “human.” On the one hand, the term can be used in a strict biological sense, so that it refers to members of the species Homo sapiens; on the other, it may refer to a being with those qualities which are distinctive of our species—in particular, the superior mental capacities that are characteristic of our species. Problems arise in both lines of response.

If the claim is that mere membership in the species Homo sapiens is enough to entitle a being to special moral consideration, we can reasonably ask why this should be so. Imagine that, as happens so often in science fiction, a good friend suddenly reveals that she is an alien who was stranded on earth when her spaceship crashed. Although she has been deceiving us all these years about her origins and her species, there was no deception in her visible delight in fresh spring mornings, her sorrow when she felt unloved, her concern for her friends, her dread of the dentist—all these feelings are real. Does our discovery