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'Pleasures', 'Pains' and Animal Welfare: Toward a Natural History of Affect

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KEYWORDS

affect, animal welfare, emotion, evolution, fitness, motivation, suffering

ABSTRACT

In hedonic theories of motivation, 'motivational affective states' (MASs) are typically seen as adaptations which motivate certain types of behaviour, especially in situations where a flexible or learned response is more adaptive than a rigid or reflexive one. MASs can be negative (eg unpleasant feelings of hunger or pain) or positive (eg pleasant feelings associated with eating and playing). Hedonic theories often portray negative and positive MASs as opposite ends of a one-dimensional scale.

We suggest that natural selection has favoured negative and positive affect as separate processes to solve two different types of motivational problems. We propose that negative MASs (eg thirst, fear) evolved in response to 'need situations' where the fitness benefit of an action has increased, often because the action is needed to cope with a threat to survival or reproductive success. We propose that these negative MASs develop in response to a change in the body (eg dehydration) or the environment (eg the approach of a predator) which creates the need for action, and that negative MASs can become intense and prolonged if the threat to fitness is high and persistent. We propose that positive MASs evolved in 'opportunity situations' where an action (eg playing, exploring) has become advantageous because the fitness cost of performing it has declined. We propose that these positive MASs occur during, or as a result of, the performance of types of behaviour which are beneficial for fitness at a variety of times, not only when they are required to meet immediate needs; and that the pleasure inherent in the behavior motivates the animal to perform it when the cost of so doing is sufficiently low. Some behavior (eg eating) can be motivated by both positive and negative affect. Other behaviour, such as playing or fleeing from a predator, may be motivated largely by positive or negative affect alone. Our hypothesis needs to be tested. but we suggest that it corresponds well to common human experience.

The hypothesis provides a basis for predicting whether an aspect of animal management is likely to cause strong and prolonged negative affect ('suffering'), or to prevent animals from experiencing certain types of pleasure. This distinction is important for bringing animal welfare assessment into line with ethical concerns.

Introduction

'Pleasures' and 'pains', or (more prosaically) positive and negative affective states, have played a key role in human thinking about animal behaviour throughout most of history. Aristotle, in his *History of Animals*, wrote that 'all animals pursue pleasure in keeping with their nature'. In the 17th century, Descartes,

although often blamed for the view that animals are without feeling, actually wrote about fear, hope and joy as motivating the behaviour of animals (Kenny 1970). In the Age of Enlightenment, Hume (1777) noted that 'love and hatred are common to the whole sensitive creation' Bentham (1823) emphasized the importance of 'pleasures' and 'pains' in motivation. Bentham's pleasures included those derived from satisfying hunger and thirst, from sexual experiences, from health, and from gratifying curiosity; his pains included feelings arising from disappointment, hunger, thirst, disease, and excessive heat and cold.

Spencer (1855) put these ideas into a more biological context by proposing that 'feelings' are adaptations. He considered that feelings, in which he included 'every species of emotion', combine with memory and reason to allow an animal to substitute flexible, adaptive reactions for merely reflexive ones. Subsequently, in the wake of Darwin's theory of evolution, it became common to view emotions and other mental states of animals as adaptive products of natural selection. For example, Romanes (1884) wrote: 'Pleasures and Pains must have been evolved as the subjective accompaniment of processes which are respectively beneficial or injurious to the organism, and so evolved for the purpose or to the end that the organism should seek the one and shun the other.'

However, it was William McDougall who proposed an explicit theory of motivation based on affective experiences. McDougall (1926) analysed behaviour in terms of motivational systems (which he called 'instincts'), governing such activities as escape from danger, sexual activity, and care of offspring. McDougall proposed that such 'instincts' are not just chains of reflexes, occurring through the automatic firing of a system of neurons, but rather are based on the animal's having subjective experiences such as fear, sexual desire and maternal tenderness, which he collectively termed 'emotions'. In essence, McDougall re-defined 'emotion' as an affective experience that motivates behaviour.

During the mid-twentieth century, the paradigm that culminated with McDougall was largely replaced by Positivist thinking, which generally limited scientific consideration to observable behaviour and avoided theories of animal motivation that included subjective experience (Rollin 1990; Burkhardt 1997). Nevertheless, the continued use of terms such as 'fear', 'hunger', 'pain', and 'frustration' in the animal behaviour literature (eg McFarland 1981) suggests that the affective states of animals remained implicitly involved in scientific thinking about behaviour, and a few scientists were entirely explicit in postulating a central role for affective states in motivation. For example, Young (1959) proposed that 'affective processes regulate and direct behaviour according to the principle of maximizing the positive and minimizing the negative'; Solomon & Corbit (1974) proposed a theory of motivation based on 'opposing' positive and negative affective states; and Herrnstein (1977) proposed that certain types of behaviour are 'self-reinforcing' rather than 'hedonically neutral' (see Toates [1986] for a review).

In the various hedonic theories, positive and negative affect have often been portrayed as simple opposites or opposite ends of a scale. For example, Young (1959) depicted a 'hedonic continuum' ranging from strongly positive to strongly negative affect (Figure 1a); Toates (1987) proposed that 'the animal is caused to move in a gradient, towards the attainment of positive affective states and the avoidance of negative ones'; and Cabanac (1992) saw the balance of pleasure and displeasure as a scale that serves as the 'common motivational currency' for deciding between alternative actions.

However, some observations suggest that a two-dimensional scale (Figure 1b), with positive and negative affect as separable phenomena, may be more correct. Animal studies suggest that the motivation that underlies eating involves two separate components which Berridge (1996) has characterized as 'wanting' to eat (ie appetite or craving) and 'liking' to eat (ie the pleasure of eating), and which appear to involve separate brain substrates. Moreover, common human experience suggests that certain types of behaviour are motivated mainly by positive states and some mainly by negative states, while others can be motivated by both. The numbered lines of Figure 1b illustrates three examples. (1) Starting in an

unpleasant state such as pain, we may act (eg by taking the weight off an injured foot) in a way which reduces an unpleasant state, but which does not provide a specifically pleasant one. (2) Starting in a neutral affective state, we may behave (eg by playing) in a manner that creates positive affect (enjoyment), with little or no negative state motivating the behaviour. (3) Starting in a negative state, such as hunger, we may act (by eating) in a manner which both relieves the negative state and creates a positive one (the pleasure associated with eating). Our first purpose in this paper is to advance an evolutionary hypothesis that tries to answer the question: why has natural selection sometimes favoured positive affective experiences, sometimes negative affective experiences, and sometimes both in the motivation of behaviour?

An understanding of positive and negative affect in animals is important in evaluating concerns over animal welfare. Public dialogue on animal welfare reveals widely held ethical priorities related to the subjective experiences of animals (Duncan & Fraser 1997; Fraser *et al* 1997). Specifically it appears: (i) that minimizing suffering (strong, negative affective states such as severe hunger, pain, or fear) is of primary concern; (ii) that allowing animals to experience normal pleasures of life is considered relevant to welfare but of lower priority than prevention of suffering; and (iii) that factors producing no affective response in the animal are seen as either not relevant (Duncan 1996) or of reduced relevance to animal welfare (Duncan & Dawkins 1983). However, existing recommendations and legislation to promote humane management of animals often seem little more than an assortment of items favouring more 'natural' behavior or more traditional rearing environments. To properly assess the ethical acceptability of alternative forms of animal management, we need some basis for judging whether a situation is likely to cause animals to suffer, or whether it prevents certain types of pleasure, or whether it has no influence on affective experience. Thus our second purpose is to propose criteria for predicting whether a situation is likely to involve negative or positive affective experiences, and to explore the resulting implications for the assessment of animal welfare.

The role of positive and negative affect in motivation: the hypothesis

Motivational affective states

We follow Spencer, Romanes, McDougall and some more recent theorists in presuming that affective states play a role in the causation of some important types of behaviour, at least among higher vertebrates. This position is not a 'theory' in the traditional sense, because it is not ultimately testable or refutable. Rather it is a 'stance' in the sense of a strategy that we adopt to predict and explain behaviour (Haugeland 1993), or a conceptual framework within which we interpret observations and propose further empirical study (Dennett 1987). It differs from the stance of many ethologists (Burkhardt 1997) and the Behaviourists (Rollin 1990) who attempted to explain behaviour without reference to affective experience.

We will use the term 'motivational affective state' (MAS) to refer to subjective states (i) that involve positive or negative affect (that is, states that are experienced as either pleasant or unpleasant, not hedonically neutral); (ii) that are involved in motivating specific types of behaviour; and (iii) that can plausibly be seen as adaptations, produced through natural selection because their influence on behaviour is adaptive - or arguably was adaptive at some time during the animal's evolutionary history. We include as negative MASs states such as hunger and fear which we presume to play a role in the motivation of eating and escape, respectively. We include as positive MASs the pleasure that may accompany such behaviours as eating, playing and mating.

MASs correspond closely to McDougall's 'emotions', and to Spencer's 'feelings', but we have avoided using these terms because of the variety of meanings that they carry. Many psychologists distinguish between 'drives' such as hunger, which arise from organic processes in the body and follow a cyclical

pattern of occurrence, and 'emotions' such as fear, which are stimulated by events outside the body and are not cyclical in occurrence (eg Izard 1993). Following Bindra (1969) and others, we draw no such sharp distinction; hence our MASs include (in Izard's terms) both 'drives' and 'emotions'.

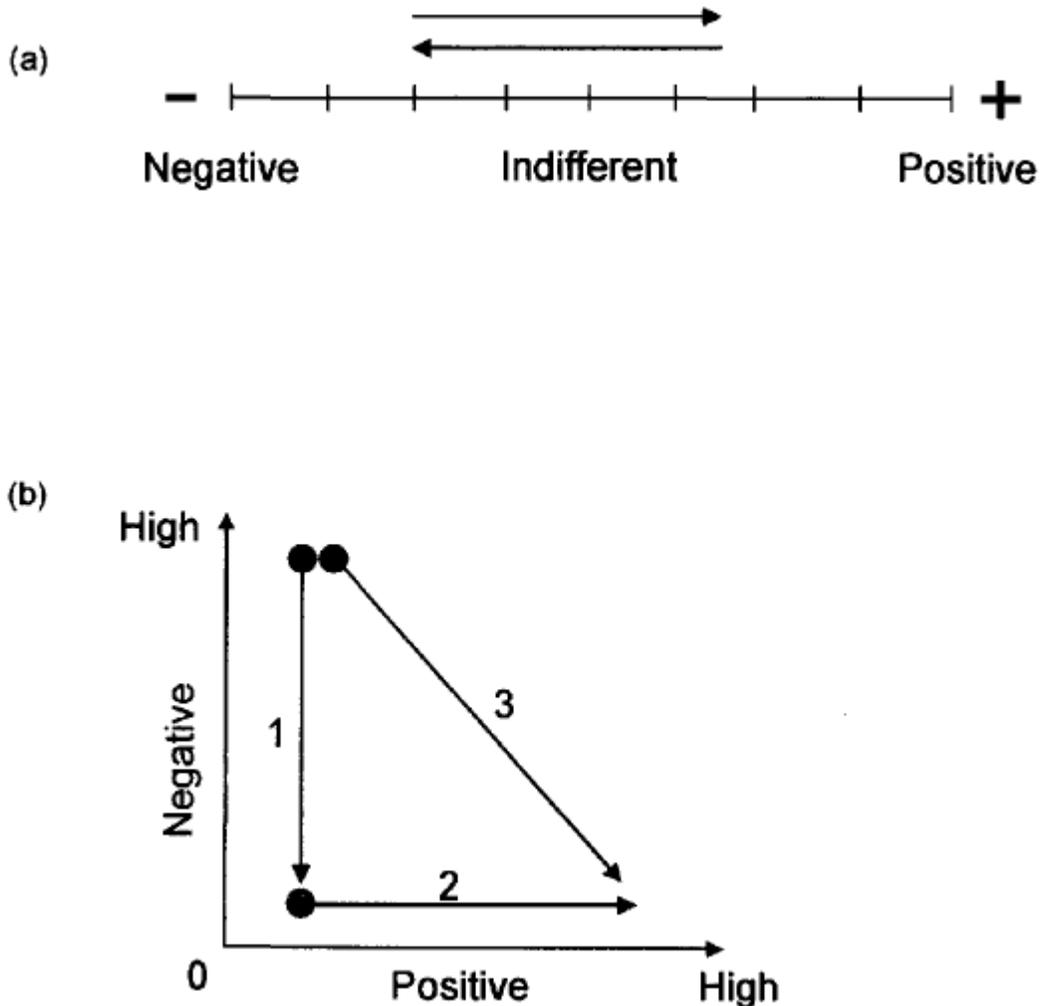


Figure 1. Two schematic representations of the role of positive and negative affect in the motivation of behaviour. (a) The 'hedonic continuum' of Young (1959) depicting transitions between positive and negative affective states as a one-dimensional scale. (b) An alternative two-dimensional depiction showing positive and negative affect as separate scales

Positive and negative MASs are not always clearly separable, and in some cases may be inextricably linked. In eating, for example, it may be impossible in some cases to separate the pleasure derived from eating food (a positive MAS) from the reduction of feelings of hunger (a negative MAS). (See also Toates [1986], on the difficulty of separating oral from post-ingestion cues in food reward.) Furthermore, the cessation of pain, nausea, or fear may bring a sense of relief that is hedonically positive (Solomon & Corbit 1974; Gray 1987). As noted above, however, many types of behaviour appear to be based

predominantly on a negative state such as pain or fear, or predominantly on a positive state such as the pleasure of playing or exploring.

'Needs' and 'opportunities'

Motivational systems favoured by natural selection should cause animals to perform an action in situations where the fitness benefit derived from the action would usually outweigh the fitness cost of performing it. We will refer to the 'net value' of performing an action at a given time as the difference between the fitness benefit and the fitness cost. Hence, we expect that evolved motivational systems will encourage the performance of actions in situations where their net value would usually be positive.

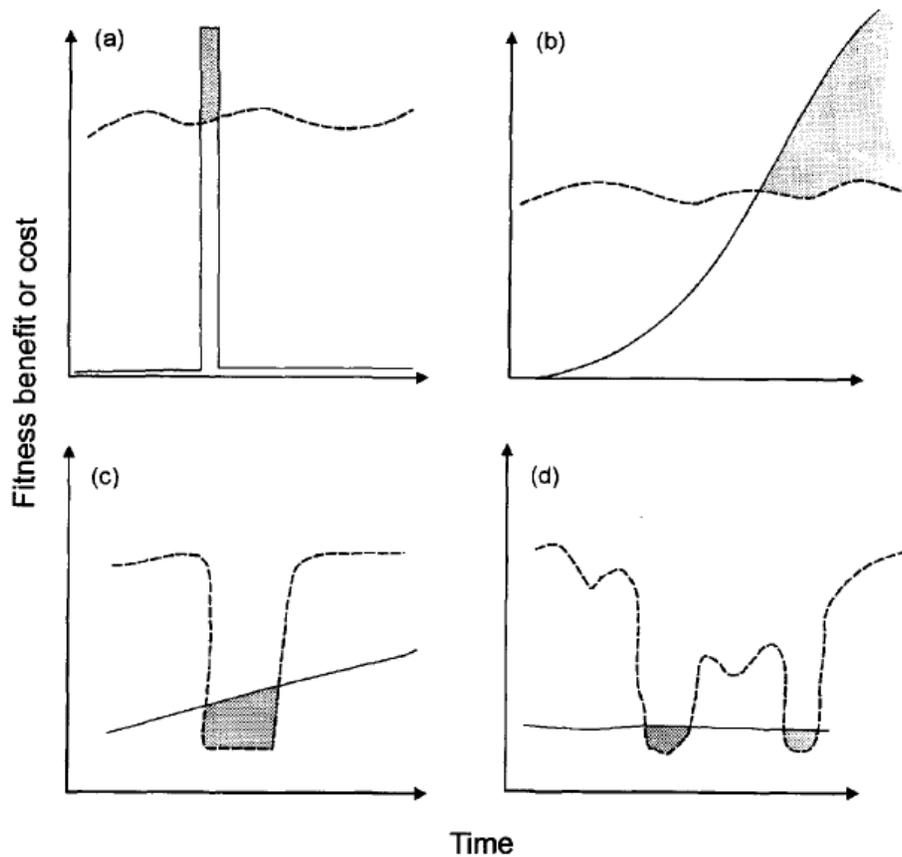


Figure 2. Hypothetical patterns of change over time in the fitness benefit (solid line) and fitness cost (broken line) of performing an action, shown in arbitrary units. In the different cases, the benefit of the action may exceed the cost (shown by shaded areas) mainly because of an increase in the benefit (a and b), or mainly because of a decrease in the cost (c and d). Examples might be as follows: (a) for a cow moose, to attack wolves would normally be of high potential cost and no benefit, but the benefit might become very great during those minutes or hours when the wolves are menacing her calf; (b) the benefit of finding water can be expected to increase from zero to very high over the course of several days as an animal becomes increasingly dehydrated, while the cost of finding water may remain relatively constant; (c) for a squirrel, the benefit of storing food may increase gradually as winter approaches; the cost may be relatively high except at times when a rich food supply (eg a mature nut crop) becomes available nearby; (d) for young animals, vigorous play may be of small, positive benefit for locomotor development; the cost of playing can be expected to fluctuate over the course of hours or days, becoming low at times when more urgent needs for food and safety have been met.

In certain situations, the net value of an action may become positive because the benefit derived from the action has increased, and not because the cost of performing it has declined. Increased benefit may occur because of a change in the environment (eg approach of a predator, Figure 2a), or because of a change in the animal's internal state (eg increasing dehydration, Figure 2b). McNamara & Houston (1986) note that behaviour is beneficial in such situations in that it is needed to cope with some threat to survival or reproductive success - in other words, failure to act would incur a fitness cost. Noting this point, we will use the term 'need situations' for cases where the net value of an action has become positive through an increase in its benefit, often because the action is needed to cope with a threat to survival or reproductive success.

In other situations, the net value of an action will become positive because the cost of performing it has declined. This will apply especially to actions whose benefits are not closely tied to immediate threats to fitness. For example, an animal may gain fitness benefits by storing food for future use, by improving motor skills through play, or by maintaining fur or feather condition through grooming. The benefit of these actions may fluctuate over time. For example, grooming may be of little benefit if the animal has just finished a bout of the behaviour; and the benefit of storing food may increase as winter approaches. However, the benefit of the behavior may rarely, or never, be high at any specific time; hence, performance of the behaviour should remain a lower priority than solving more immediate threats to survival and reproductive success (see Martin & Caro 1985 on play). However, the cost of performing such activities may decline substantially from time to time. For example, the cost of storing food may suddenly drop because a rich food supply has become available nearby (Figure 2c), or the cost of playing or grooming may become very low when no danger is present and the animal's other needs are fully met (Figure 2d). We will refer to 'opportunity situations' where the net value of an action has become positive because the cost of performing it has decreased.

In most real situations, both the benefit and cost of an action are likely to vary over a range of values. Hence, we use 'need situation' and 'opportunity situation' as a shorthand to refer to the two extremes of the variation, and we do not imply that all situations fall neatly into one category or the other.

Different motivation for need and opportunity situations

We propose that need and opportunity situations create two different and complementary types of problems in the motivation of behaviour.

To respond to need situations, animals should be motivated to take an action when its benefit has increased, often because of a threat to survival or reproductive success. We propose that in higher vertebrates, the motivation to respond to need situations is commonly based on negative MASs such as thirst and fear which the animal tries to reduce or eliminate, and that these states have the following properties:

- § 1(i) They develop in response to situations where the benefit of the action has increased, often because the action is needed to cope with a threat to fitness. The threat may arise from a change in the body (eg dehydration, producing the negative MAS of thirst) or in the environment (eg approach of a predator, producing the negative MAS of fear).
- § 2(ii) They persist as long as the need situation continues.
- § 3(iii) They vary in strength depending on the degree of benefit that the action would normally bring in that situation (ie the severity of the threat to fitness that the situation normally entails).

Some need situations last for a considerable time and entail severe threats to fitness, as in slow death by starvation. Our proposal implies that negative MASs can provide a sustained motivation to take corrective action as long as such a situation persists, and that this motivation can become very strong when the threat to fitness is great.

To deal with opportunity situations, animals should be motivated to perform actions whose net value has become positive because the cost of performance has declined, but not at other times. We propose that in higher vertebrates the motivation to respond to opportunity situations is commonly based on positive MASs, such as the pleasure of playing or eating, which the animal tries to experience, and which have the following properties:

- § 2 (i) They occur during, or as a short-term consequence of, the performance of types of behaviour that can be beneficial at a variety of times, not only when specific need situations arise.
- § 2 (ii) They persist while the beneficial action is being performed and/or for a short time thereafter.
- § 2 (iii) They vary in strength depending on the likely benefit of the behaviour at the time, dropping to zero in situations where the behaviour would normally be of no benefit.

This proposal implies that the pleasure normally inherent in, or resulting from, certain activities contributes to a 'motivational state' (in the sense of McFarland 1985) which influences, but does not directly determine, whether the behaviour will be performed. The actual decision to perform the behaviour at any given moment will thus depend on the balance of this hedonic motivation against the apparent cost (eg difficulty or perceived danger) of performing the behaviour, such that the behaviour is likely to be performed at times when the cost is sufficiently low.

In certain respects, positive and negative MASs function in similar ways. Presumably, either can motivate by anticipation. For example, an animal may anticipate pain in an avoidance-learning task and act to prevent it; or an overheated person may anticipate the pleasure of drinking a cool liquid and act so as to obtain it. Similarly, a decision to stop or continue an ongoing action may be influenced by either a positive or negative MAS: an animal may feel pain from running on an injured foot and consequently stop running; or it may feel pleasure at eating a palatable food and continue to eat it. However, negative MASs have an additional property because they are tied to situations rather than the performance of actions. For example, an animal may feel fear when faced with a predator, or may feel thirsty as the body becomes dehydrated, and these negative MASs may then stimulate the animal to initiate some action to cope with the situation.

In proposing that affective states play a role in motivation, we do not suggest that all behaviour is caused by affective states. Much behaviour may be performed in a reflexive manner without affect (eg Epstein 1982), or it may become habitual and be performed in the absence of affect.

Nor do we suggest that all types or all occurrences of affect are adaptive. Non-adaptive examples may arise for several reasons. (i) In any given situation, the actual fitness benefit and cost of an action may be impossible to assess; hence we expect MASs to develop according to certain 'rules of thumb' which are adaptive on average but need not be adaptive in all circumstances (Stephens & Krebs 1986). For example, we do not presume that an actual fitness cost is incurred each time an animal is sufficiently dehydrated to feel thirsty, but rather that it is adaptive for an animal as a rule to experience thirst, and thus be motivated to seek water, as dehydration develops. (ii) These 'rules of thumb' may not be adaptive if animals are kept in an environment unlike that in which their ancestors evolved. For example, pleasure associated with eating sweet food may have been adaptive for a species in its ancestral environment but not for the same species in an artificial environment where sweet food is abundant. (iii) The capacity to

experience affective states may be adaptive partly because it allows an animal to learn to respond to its individual circumstances, for example by acquiring learned fears; however, not all the learned fears that an animal acquires will necessarily be adaptive. (iv) Finally, it is not clear whether the human capacity to experience certain affective states (eg despondency, guilt, anxiety) evolved because these states may at times be adaptive (eg despondency may help conserve energy) or whether they are merely by-products of a capacity for affective experience.

Testing the hypothesis against human experience

The best tests of this hypothesis could be made through research on humans, who can report on their affective experiences. Ideally, this should involve systematic research methods like those of Young (1973) and Cabanac (1992). Pending such work, we offer the following observations on what we believe to be common human experiences, and we encourage readers to test these against their own subjective experiences.

Consistent with § 1(i), we believe that situations which normally create a need to act in order to cope with a threat to fitness do tend to give rise to negative MASs. Potentially damaging disturbances to homeostasis give rise to negative MASs such as hunger, thirst, cold, and the distress associated with an inability to breathe. Situations involving injury or danger of injury, where behaviour is needed to protect the body from harm, also typically involve negative states such as pain and fear. Substantial threats to reproductive success tend to produce strongly negative states in humans. In particular, human parents experience great distress if they lose track of young offspring, and individuals may experience distress when faced with desertion by an actual or potential sexual partner.

Consistent with § 1(ii), we think that in human experience, negative states can become very persistent if a need situation (eg a threat to survival or reproductive success) continues. Rage over desertion by a spouse, and anxiety over disappearance of children, can persist for months or years. Hunger may seem to be an exception because feelings of hunger come and go during a period of food deprivation, and may decrease during a prolonged fast. However, a severe restriction of food intake (which seems more likely to have occurred in human evolutionary history than prolonged fasting) is said to maintain 'a continuous highly painful sensation of hunger' (Le Magnen 1985).

Consistent with § 1(iii), we think that human experience largely confirms that negative MASs vary in strength, roughly in relation to the potential benefit of the action (or the threat to fitness), at least for the kinds of situations where there is some basis for predicting the severity of the threat to fitness. Feelings of thirst, cold, and pain can range from mild to extremely intense, and within limits these appear to vary with the severity of the underlying challenge. For circumstances producing fear or jealousy, however, the severity of the threat to fitness may be impossible to assess and the intensity of the experience may be poorly linked to the actual severity. Hence, we may expect seemingly 'irrational' fear or jealousy to be more common than, say, 'irrational' thirst.

Consistent with § 2(i), we suggest that positive MASs largely occur during, or as a result of, performance of actions whose benefits are not limited to specific need situations. Play, exploration, and normal social contacts with family and community members may well convey benefits, but these activities are not generally needed to respond to short-term threats to fitness; these activities do appear to be motivated largely by the pleasure inherent in the activities or their consequences. In contrast, actions which contribute positively to fitness only in specific circumstances (fleeing from danger, limping) tend not to be pleasurable in themselves.

Consistent with § 2(ii), we suggest that the pleasure of hedonically positive activities does tend to occur during or soon after the performance of the behaviour, and thus does not form a highly persistent affective experience as do negative states such as hunger or fear.

Consistent with § 2(iii), we think that in human experience, the strength of positive MASs does vary roughly with the degree of benefit likely to be derived from the behaviour in the situation. Behaviour with a large potential fitness benefit (eg bonding with a potential mate) can involve intensely positive affect. Furthermore, the pleasure of an action can drop to zero in situations where the action would make no contribution to fitness. Rough-and-tumble play is presumably of some benefit to children during locomotor development but not to elderly people, and such play appears to be pleasurable to children but not to the elderly.

Finally, consistent with § 1 (i) and § 2(i), we suggest that behaviour that can have a positive effect on fitness in both need and opportunity situations tends to be motivated by both negative and positive MASs. Eating and resting can be adaptive in need situations to prevent serious depletion of body resources, and in such cases can be motivated by the unpleasant states of hunger and fatigue. At other times, eating and resting can also be of benefit as ways of keeping the body well-nourished and rested, and these behaviours tend to be pleasurable to perform in the absence of a corresponding negative MAS.

Application to animal welfare assessment

As noted above, public priorities regarding animal welfare appear to be, in descending order: (i) that animals should not be kept in situations causing intense and prolonged unpleasant affective states; (ii) that animals should be permitted normal pleasures; and (iii) that situations where neither positive nor negative affect is involved are of less or no concern. Our hypothesis suggests a means of judging into which of these categories a given situation is likely to fall.

According to the hypothesis, where life history data suggest that a situation would normally require animals to take some action to cope with a threat to fitness (or, more precisely, where this was probably the case during the animal's evolutionary history), then we expect that situation to give rise to a negative affective state. Furthermore, if the potential threat to fitness is great, and if the situation persists, then the negative state should become sufficiently intense and prolonged to provide a sustained, high level of motivation to act. This might be evidenced, for example, by repeated attempts to perform the behaviour, by emotional vocalizations, or by indicators of high motivation strength in an instrumental conditioning test (eg Dawkins 1990; Duncan 1992; Fraser 1993). Affective states in this category will include those that equip an animal to deal with immediate threats to safety (eg fear), to homeostasis (eg hunger), and to reproductive success (eg distress over separation from offspring).

However, if a type of behaviour is performed when the cost of performance is low, not when it is needed to cope with a situation involving some threat to fitness, then the behaviour is likely to be motivated by a positive affective state which accompanies its performance. This category will probably include many forms of natural behaviour such as play, exploration, and social grooming, which animals will perform when the cost of performance is low but curtail when the cost is increased (Dawkins 1990).

In cases where an animal has had no control over a factor in its environment, we expect neither a positive nor a negative MAS to have evolved. For example, most animals that do not use caves or burrows have had little means, during their evolution, to control the amount of ambient light in which they live, and we do not expect them to have evolved a positive or negative affective state to motivate them to achieve a certain light intensity in their environment. In such instances, animals would be expected to show no strong motivation in, say, an instrumental conditioning test.

Thus, we propose that life history information can help to predict where potential animal welfare issues are likely to fall within the three priorities listed above, as a hypothesis for empirical study. The following examples illustrate the approach.

Although domestic piglets spend considerable time suckling at the sow's udder, they receive milk only during brief milk ejections that last about 10-20 s and that occur about once per hour during coordinated suckling by the entire litter (Fraser 1980). Piglets that fail to suck in these 10-20 s do not obtain milk, and repeated failure can lead to death by starvation or to serious retardation of growth (Fraser 1990). Thus, habitual failure to find and suckle a teat when the rest of the litter is suckling involves a severe threat to fitness. Our hypothesis predicts that pigs will have evolved a negative MAS which is experienced by the young if they are prevented from suckling when a nursing episode is in progress. Behavioural observations are consistent with this view: unlike young mammals of many other species, piglets prevented from participating in a suckling episode become extremely active and aggressive; they give and receive significant facial lacerations in trying to gain access to teats; and they make loud, scream-like vocalizations if prevented from using their habitual teats (Fraser 1975). Moreover, pigs appear to retain into adulthood a similar tendency to evidence distress if they cannot eat when food is provided to their group mates, as indicated by loud vocalization and intense activity in group-feeding situations where some individuals are excluded. In some swine husbandry systems, animals are often excluded from group-feeding situations, for example if a food delivery system allows some but not all group members to eat simultaneously, or if a farrowing pen blocks the piglets' access to some of the teats when a nursing is in progress (Fraser & Thompson 1986). The above reasoning suggests that pigs in these situations will experience a strong negative affective state.

For jungle fowl, *Gallus gallus*, the putative progenitor of domestic fowl, the selection of a suitable nest site and the building of a nest before laying an egg are vital for reproductive success. Moreover, nesting behaviour in domestic hens is triggered by events at ovulation, about 24h before nesting and laying (Gilbert & Wood-Gush 1965). The hen has only limited control over the timing of laying, and if an egg is retained too long in the shell gland, extra calcium is deposited on the shell, and the succeeding egg in the clutch is likely to be misshapen (Hughes *et al* 1986), both of which events reduce hatchability. Thus habitual failure to select a nest site and build a nest in the brief pre-laying period would entail an appreciable threat to fitness. According to the hypothesis, the behaviour should be motivated by a negative MAS. Observations on hens in battery cages are consistent with this view. The battery cage does not seem to provide the key stimuli necessary to elicit the sitting component of nesting behavior in many hens of light (body weight) hybrid strains (Wood-Gush 1969; Wood-Gush & Gilbert 1969) and these birds show symptoms of severe frustration in the pre-laying period (Duncan 1970). Furthermore, studies measuring the hen's motivation to nest, for instance by placing various obstacles between the hen and a nest site, indicate that hens in the pre-laying period have a high level of motivation to gain access to a nest site, equivalent to their motivation to reach food after many hours of food deprivation (Duncan & Kite 1987; Follensbee *et al* 1992).

As a third example, rooting and chewing on objects in the environment are major components of the foraging behaviour of pigs, and feral pigs will spend some hours each day in these activities. For a well-fed animal, the benefit of foraging presumably does not depend greatly on the behaviour being performed at specific times. We would expect, therefore, that for well-fed pigs, rooting and chewing should be pleasurable activities, but a lack of opportunity for these activities should not cause a negative MAS. Behavioural observations are consistent with this view. When provided with fresh straw (a preferred substrate for rooting and chewing), well-fed pigs are clearly attracted to it and spend considerable time in these activities, but an absence of straw does not by itself lead to signs of agitation or disturbance (Fraser *et al* 1991). With poorly fed pigs the situation is different. Failure to look for food when poorly fed would

presumably entail a threat to fitness, and natural selection should favour a negative MAS that motivates food-deprived animals to forage. Again, behavioural observations are consistent with this view. Pregnant sows are often raised on limited rations which have been shown to produce chronic motivation to eat (Lawrence *et al* 1988). Such animals show considerable behavioural disturbance if prevented from foraging (Appleby & Lawrence 1987), and provision of foraging opportunities reduces these disturbed activities.

Animal welfare implications

Discussion about the welfare of animals often arises because of a concern that animals will suffer when kept in restrictive, unnatural or unpreferred environments, or in environments where they are unable to perform their natural behaviour. We suggest that some of these situations will indeed cause animals to suffer (in the sense of experiencing intense and prolonged unpleasant states), while others may only prevent animals from experiencing certain pleasures, and yet others may have little or no effect on the animals' affective experience.

In trying to assess how different situations affect animal welfare, researchers have proposed various criteria based on tests of motivation strength, choices made in preference experiments, performance of natural behaviour, the incidence of stereotypies, and the degree to which animals live in accordance with their naturally selected decision rules (Dawkins 1980;1990; Duncan 1992; Duncan & Dawkins 1983; Broom 1991; Broom and Johnson 1993; Fraser 1993; Barnard & Hurst 1996). However, to link these criteria to the ethical concerns that gave rise to animal welfare research, we need to be more explicit on how the behavioural biology of animals is related to their affective experiences.

Our hypothesis is an attempt to make this link more explicit. Most importantly, we propose that the affective states which are of greatest ethical concern - prolonged, intense, negative states - evolved in response to those life history situations where animals would normally need to act in order to cope with a threat to fitness, whereas states involving pleasure evolved in response to situations where animals could, on average, gain a fitness advantage by performing actions at times when the cost of acting is low. Recommendations and regulations for improved animal welfare could usefully be evaluated in this light.

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