

WELFARE BY DESIGN: THE NATURAL SELECTION OF WELFARE CRITERIA

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Final acceptance: 10 June 1996

Abstract

Animal Welfare 1996, 5: 405-433

The scientific study of animal welfare has generated a welter of complex, equivocal and often contradictory results. Consequently, there is little agreement about how impairment of welfare should be measured. While some solutions to this have been suggested, these have usually relied on more sophisticated versions of, or more control over, existing measures. However, we argue that the difficulties arise because of questionable assumptions in the definition and measurement of welfare, in particular the measurement of suffering and the assumed importance of individual well-being. We contend that welfare can be interpreted only in terms of what natural selection has designed an organism to do and how circumstances impinge on its functional design. Organisms are designed for self-expenditure and the relative importance of self-preservation and survival, and the concomitant investment of time and resources in different activities, varies with life history strategy. The traditional notions of coping and stress are anthropomorphisms based on homeostatic mechanisms of self-preservation in a long-lived species. Suffering-like states are viewed as generalized subjective states that are geared to avoiding deleterious circumstances with which the organism does not have specific adaptive mechanisms to deal. Attempts to measure suffering-like states directly are likely to remain inconclusive, at least for the foreseeable future, because such states are private and subjective, may take many forms fundamentally different from our own and are likely to depend on the operation of phenotype-limited priorities and decision rules. However, measuring the impact of circumstances on functional design via the organism's decision rules provides a practicable means of giving benefit of the doubt by indicating when suffering, or an analogous subjective state, is likely.

Keywords: *animal welfare, anthropomorphism, coping, decision rules, fitness, life history, measurement, stress, suffering*

Introduction

The welfare of animals, especially in the contexts of management and exploitation is currently a prominent and emotive subject of public concern. Largely, though not entirely, for this reason it is also the focus of intense scientific attention. As Mason & Mendl (1993) have pointed out recently, however, the attempts of science to introduce objectivity into decisions about welfare have generated a welter of complex, equivocal and often contradictory results, a concern that has been echoed by several other authors (eg Rushen

1986; Dawkins 1990; Mendl 1991; Rushen & de Passillé 1992; Manser 1992; Broom & Johnson 1993; Fraser 1993, 1995). While various authors suggest reasons for, and some solutions to, these difficulties, the conclusion is generally that more sophisticated versions of existing measures of welfare, or more careful control over existing measures, would largely overcome them (Mason & Mendl 1993). We argue here that the difficulties arise as a result of questionable assumptions in the definition and measurement of welfare, and that attempts to overcome them hitherto have treated the symptoms of the problem rather than its cause. We contend that current approaches to welfare flounder because of unnecessary concern with measuring suffering and an anthropomorphic perspective on the importance of individual well-being. Careful consideration of these problems from an evolutionary perspective leads to a more robust basis for judging welfare which questions traditional views of individual well-being and the related notions of coping and stress.

Defining and measuring welfare

There is little agreement about how welfare should be defined (Rushen & de Passillé 1992). Most attempts fall into one or more anthropomorphic categories (Moberg 1993) that broadly emphasize comfort (the extent to which the animal is maintained in adequately spacious conditions with basic requirements readily available, eg Wolfensohn & Lloyd 1994), health (the extent to which it is maintained hygienically and free from infection, injury, 'stress' and psychological abnormality, eg Broom 1991; Hurnik 1988), normality of opportunity (maintenance in circumstances that allow a natural range of behaviours and provide a natural social, sexual and reproductive environment, eg Thorpe 1965; Martin 1975) or philosophical stances on ethics and animal rights (Rollin 1981, 1993; Midgely 1983; Regan 1984). Such criteria, for example, form the basis of the so-called 'five freedoms' proposed by the UK Farm Animal Welfare Council (Harrison 1988). Within these, there is a broad division between viewpoints that emphasize apparent or putative emotional suffering (Griffin 1981; Rollin 1989; Duncan & Petherick 1991; Duncan 1993) and those that emphasize impairment or enhancement of biological functioning (Broom 1991; Hurnik 1988; Loliger 1985; see Rushen & de Passillé 1992). These, of course, are not strictly alternatives (see also Fraser 1993, 1995). Because emotional suffering is a private, subjective experience, arguments based on it necessarily rely for support on measures of function or performance as indirect indicators of suffering (Dawkins 1993). In addition, from an evolutionary perspective, positive and negative subjective experiences can be viewed as proximate mechanisms regulating the animal's exposure to circumstances that enhance or impair its reproductive potential, and thus as being directly associated with changes (or the likelihood of changes) at the level of biological functioning. This association between function and putative mechanism, however, is not straightforward (van Rooijen 1981; McFarland 1989; Dawkins 1990). It is therefore helpful briefly to clarify the assumptions behind it and its implications for the study of welfare.

Biological function and subjective states

Figure 1 summarizes the interrelationships between the functional and subjective state lines of argument and Table 1 the kinds of measure used to infer effects on function and subjective state. From the functional viewpoint, the decisions an organism makes have consequences

for its reproductive potential, many via effects on maintaining the integrity and survival of the individual (through reducing physiological deficits, avoiding danger etc).

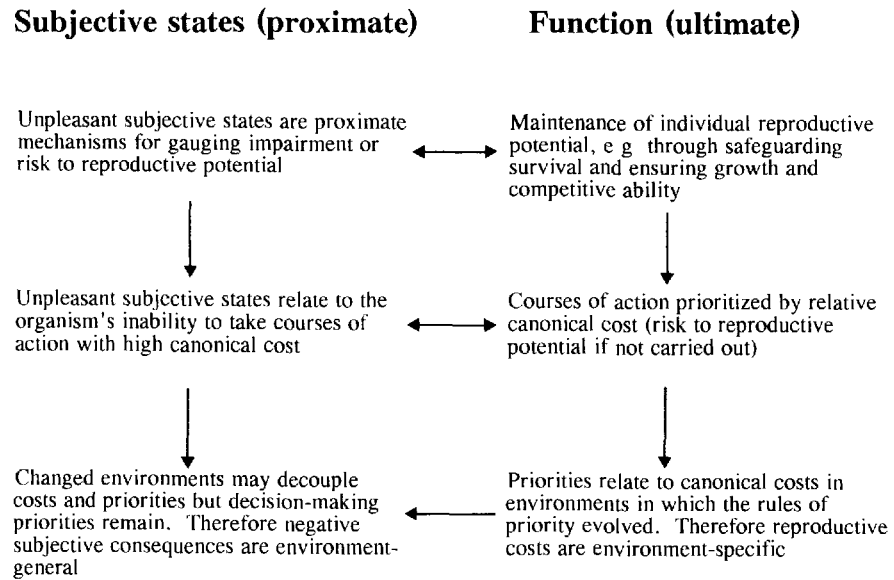


Figure 1 Postulated relationships between the functional state of an organism and its possible subjective experience. From discussion in McFarland and Houston (1981), McFarland (1989) and Dawkins (1990). See text.

Table 1 Measures used to assess an organism's priorities and the impact of circumstances on its functional and putative subjective welfare. From discussion in Dawkins (1988), Mason and Mendl (1993) and Broom and Johnson (1993). See text.

Subjective states (proximate)		Function (ultimate)
Welfare ≡ consequences for ability to prioritize and cope		Welfare ≡ consequences for physical function and reproductive potential
Assessing priority	Assessing impact	Assessing impact
for example	for example	for example
- behavioural resilience	- physiological stress responses	- growth
- rebound effects	- stereotypes	- longevity
- cost tolerance	- displacement activities	- offspring production
- preference tests	- repertoire size	- immunodepression
		- disease
		- injury
		- fluctuating asymmetry

Negative subjective states at this level (thirst, hunger, fear etc), if they exist, can then be viewed as proximate mechanisms registering the organism's predicament and triggering appropriate courses of action (Figure 1). The currency by which the organism measures its predicament is canonical cost (McNamara & Houston 1986), the cost to the organism's reproductive potential if its present state (physiological deficit, proximity to a predator etc) remains unchanged. Canonical cost is thus a standardized currency by which any state of the organism can be gauged and against which the organism should prioritize its physiological and behavioural decisions (McFarland 1989). The degree of unpleasantness of negative subjective experiences might therefore be expected to relate to the magnitude of the cost of the organism's current state and the extent to which circumstances frustrate its ability to prioritize its activities (Figure 1, Table 1). However, the organism's rules of priority relate to the canonical costs in the environment(s) in which the rules evolved (the *cost function* sensu McFarland & Houston 1981). The relationship between priority and cost is therefore environment-specific and the environment in question can be regarded as the organism's environment of evolutionary adaptation (EEA, see Mace 1995). Changing the environment, eg by bringing the organism into captivity, may decouple this relationship (leading to a disparity between the cost function and the organism's *objective* and *goal functions* sensu McFarland & Houston 1981), but the rules of prioritization and any subjective experiences associated with them remain. Rules of prioritization and associated subjective states therefore operate across environments (are environment-general), but their efficacy is determined by the functional similarity of the environment to the organism's EEA. Dawkins (1990) uses the example of migratory restlessness (Zugunruhe) in a captive bird. A bird of a species that usually migrates to warmer winter feeding grounds in autumn is kept in a cage. It is well cared for and is provided with plenty of food. As a result its chances of surviving the winter are far greater than those of its free-living conspecifics that migrate in the normal way. The canonical cost of not migrating is thus likely to be small. However, the bird's rules of prioritization did not evolve in a well-provisioned cage but in a seasonal environment where winter food supplies are short. As a result, the bird still shows migratory restlessness at the appropriate time and may suffer through frustration, as well as possibly exhaustion and physical injury, as a result of not being able to escape. Inglis *et al* (in press) discuss other examples in which animals choose to work in the face of a freely provided resource. While it might be argued that this kind of scenario is likely only with developmentally-fixed ('hard-wired') rules, we shall see later why it is also applicable to apparently adaptively plastic rules based on experience. The important point is that the impact of the organism's current environment on its rules of prioritization and any associated subjective states depends on the degree of departure from the organism's EEA.

Function, suffering and benefit of the doubt

It is unlikely that we shall ever have a direct and unequivocal means of appreciating the subjective experiences of other organisms, even other conspecifics. Inferences about negative subjective states in others that we might wish to compare with suffering can therefore be made only on some 'benefit of the doubt' basis. This acknowledges the ethical, 'value-laden' (Rollin 1993; see also Fraser 1995) origin of both popular and scientific concern with animal welfare and allocates to science the role of determining the best means of embracing it. The question then arises as to the criterion science should use for giving the benefit of the doubt

in any particular case. If, following the argument above, we make the reasonable assumption that suffering is an adaptive attribute of the organism shaped by natural selection to help it avoid circumstances that compromise its reproductive potential, the criteria must in some way be based on such circumstances. This means appreciating the reproductive cost of the circumstances or, more importantly as we have seen, the animal's rule of thumb estimate of the cost. (Note that we are not equating welfare with reproductive *success* (cf Mendl 1991); as has been argued thoroughly elsewhere (eg Dawkins 1980), the number of offspring an organism produces is as unreliable a measure of its welfare as any of the physiological and behavioural measures that have been debated (see below).) Since this is an evolutionary argument, the anthropomorphic criteria referred to earlier might at first sight seem reasonable. There are obvious continuities of physical form and function between ourselves and other species so, arguably, there is a fair chance of continuities in sensory and mental attributes. Indeed, as Byrne & Whiten (1988), Rollin (1989), Dawkins (1993) and others have forcefully pointed out, research is uncovering many physiological and behavioural characteristics of other organisms that increase our confidence in their experiencing related subjective worlds. While we acknowledge with Dawkins (1993) that these raise interesting possibilities for the functioning of other minds, the welfare concerns they arouse tend to be proportional to the perceived similarity with ourselves. Thus the existence in other vertebrates of central nervous system receptors for anxiolytic and analgesic chemicals leads to the suspicion that they experience anxiety and pain as we do even if they do not express them in the same way (Rollin 1989; see also Morton & Griffiths 1985). However, there are several reasons why anthropomorphism, even at this refined level, is unsafe as a basis for decisions about welfare.

Negative implications of applying anthropomorphic criteria

In the first place, it is not obvious that such criteria serve our own species well as yardsticks of welfare. So-called diseases of affluence, such as diabetes, heart disease, diseases connected with industry, some cancers and parasitic infections, as well as increasingly recognized psychological dysfunctions (eg Nelson 1972; Cornwell 1984; Showalter 1987; Desowitz 1987; Nesse & Williams 1994), are emerging costs of emphasizing 'comfort' criteria in the assessment of welfare and standards of living in human societies. In large part, of course, this is a consequence of humans living and making decisions in environments very different from their EEA, in which the relationships between pleasurable cues and adaptive outcomes have become distorted (eg the predilection for sweet confectionary). Since some of the above conditions can be replicated in other species subjected to the potential sequelae of high living standards in humans (reduced activity, rich diets etc), 'comfort' criteria form a dangerous basis for generalizing across species.

Evolutionary continuity versus adaptive divergence

A second problem, as McFarland (1989) has argued, is that the evolutionary argument for generalization is a two-edged sword. On the one hand it predicts similarity in characteristics through shared ancestry, on the other it predicts divergence between species, and even populations and individuals within species, through adaptive specialization. Thus, while there may be similarities between species at a general level that have implications for welfare (eg homology in central nervous system structures, neuronal physiology, sensory receptors), there may be adaptive differences of far greater significance (eg species-specific learning

abilities, perception and pain tolerance). This should lead us to be cautious about the concept of suffering in judging welfare. Suffering is of interest to us only because it is the subjective correlate of certain deleterious circumstances that we experience. The adaptive divergence argument calls into question the assumption that suffering in our, or indeed any, sense is a consequence of deleterious circumstances in other species. Benefit of the doubt generalization is usually justified on the basis that other species may feel pain in much the way we do (Rollin 1989), and/or that they have cognitive wants and aspirations that are similarly capable of frustration (Duncan & Petherick 1991). However, the evidence in both cases is equivocal to say the least (eg Bateson 1991; McFarland 1989; Kennedy 1992). Even where species possess similar physiological correlates of human pain sensitivity we cannot be certain that these *function* in the same way. A cautionary example from a different context is the expression of the enzyme argininosuccinate lyase (ASL) in the livers of birds and reptiles (de Pomerai *et al* 1991). ASL is more familiarly associated with the liver of mammals as a component of the mammalian urea cycle. On this evidence alone, a naïve physiologist encountering it in birds and reptiles might conclude that these groups share the same mechanism of nitrogenous excretion as mammals. Of course they do not and the enzyme has little function in this regard; in fact, the gene coding for it in birds and reptiles has been coopted for an entirely different purpose: the production of a structural protein in the lens (Piatigorsky *et al* 1988)!

At least three tenable possibilities therefore exist: a) other species can experience suffering in a form homologous with our own, b) other species experience negative subjective states that are wholly different from our own but might lead to taxon-specific forms of experience that are analogous to suffering, and c) other species do not experience negative subjective states at all and cannot be thought of as having a suffering-like state in the sense of (a) or (b) (see the discussion of procedural interpretations below). Anthropomorphic uses of the concept of suffering in welfare studies may therefore be dangerously inappropriate in particular cases. Since it is unlikely that we shall be able to distinguish reliably between (a), (b) and (c) empirically (because all three could produce identical responses to circumstance and thus confound the evidence on which we depend for inferring subjective states (Dawkins 1993)), presumed measures of suffering *per se* cannot be a criterion for gauging welfare or limiting concern about welfare to species assumed, on whatever basis, to experience suffering (cf Duncan & Petherick 1991). *Taking account of the risk of a suffering-like state sensu (a) or (b), however, is a different matter and one that we argue should form the basis for giving the benefit of the doubt, even though it may sometimes be given to organisms that have no capacity for subjective experience (though while the ethical incentive for concern may be removed in these cases, the scientific incentive may remain (see below)).*

Fitness, coping and stress: the fallacy of individual preservationism

Welfare and fitness

'Comfort' and 'health' criteria, indeed the very notions of welfare and well-being themselves, imply a high priority for the preservation and maintenance of the individual. From an evolutionary viewpoint, however, individuals are expendable commodities in the pursuit of reproductive success (Dawkins 1982; Partridge & Harvey 1988). Adaptations are costly; they 'use up' the time and metabolic resources of the individual, or risk its well-being or survival, in ways that are traded off by selection against reproductive outcome. On this view, measurable costs such as reduced growth, increased fluctuating asymmetry,

immunodepression, pathology and injury may reflect adaptive trade-offs that the organism is designed to accept. While the organism may experience negative subjective states associated with these costs (eg fatigue, pain, hunger, nausea, fear), they are part of the mechanism of naturally selected regulatory processes that optimize its activities during its lifetime rather than a reflection of circumstances in which it is not designed to be. Indiscriminate concern about such states is itself an anthropomorphism based on the self-preserving imperative of a species with a long reproductive lifespan and a long period of parental care. This anthropomorphism is compounded by the widespread tendency in the welfare (and other) literature to use 'fitness' as a property of individuals. Thus 'fitness' is equated to measures of growth, longevity, offspring production, health and so on (eg Dawkins 1990; Mendl 1991; Duncan 1993; Broom & Johnson 1993). On the argument above, however, an individual is simply an expendable vehicle for the perpetuation of strategies of response to the environment through the relative impact of different strategies on reproductive success (Dawkins 1982). 'Fitness' is therefore more accurately construed as a property of alleles coding for alternative strategies of response and thus life history investment. Responses that preserve the individual may be adaptive where reproductive success depends on longevity, but expendability and self-sacrifice are the expected features of many other life histories (see Kirkwood 1993). The use of 'fitness' at the individual level in welfare arguments is thus not just inaccurate but actively misleading since it obscures consideration of what selection has actually designed organisms to do and what their life history priorities might be. We refer to this anthropomorphic concern with the survival and maintenance of the individual as *the fallacy of individual preservationism*.

Coping and stress

The fallacy of individual preservationism is inherent in two other notions central to the concept of welfare: coping and stress. Broom and Johnson (1993) define coping to include the normal regulation of body state (through, for example, body repair systems, immunological defences, maintenance behaviours) and emergency responses (emergency physiological processes and behavioural responses). Broom defines the welfare of an animal as its 'state as regards its attempts to cope with its environment' (Broom 1986; Broom & Johnson 1993), by which he means both how much the animal has to do to cope and how well its coping attempts are succeeding. Failure to cope, or working excessively hard to maintain coping, leads to reduced welfare which will be reflected in some form of suffering (pain, anxiety, depression etc) and may lead to functional impairment (eg reduced growth or reproduction). The second notion, stress (Selye 1950; 1976), is often invoked as the cause of an animal's failure to cope or over-exertion in order to cope. 'Stress' therefore characterizes the environmental impositions, internal or external, that tax the animal's coping mechanisms and reduce its welfare (see Broom & Johnson 1993 for an extensive discussion).

While the notions of coping and stress seem at first to provide a handle on welfare, they amount to little more than conceptual labels. Attempts to define and measure them in particular cases are fraught with difficulty and disagreement (Rushen 1986, 1991; Barnett & Hemsworth 1990; Mendl 1991; Mason & Mendl 1993). This is largely because certain behavioural and physiological responses by organisms (eg stereotypies, elevated levels of glucocorticoid hormones, raised blood pressure) that have been associated with presumed stressful circumstances (eg overcrowding, isolation, exposure to aggression, electric shock treatment, restraint, see Manser 1992) have been labelled 'stress responses' and then used,

tautologically, to diagnose the existence of stress in other circumstances. The widely acknowledged problem here is that many of the responses showing some association with a presumed stressful situation may simply (or at other times) reflect the adaptive functioning of the organism rather than over-extension of coping mechanisms (Szechtman *et al* 1974; Colborn *et al* 1991; Manser 1992; Broom & Johnson 1993). Attempts to distinguish between these possibilities have resulted in largely fruitless arguments about cut-off levels of stress response in relation to welfare (Barnett & Hemsworth 1990; Mendl 1991; Gonyou 1993; Moberg 1993; McGlone 1993) and how to overcome the multitude of factors that confound simple interpretations of stress responses (Rushen 1991; Mason & Mendl 1993; Broom & Johnson 1993). In addition to these difficulties, coping is also predicated on individual preservationism since it is characterized as a homeostatic mechanism maintaining the physical, physiological and psychological integrity of the individual in the face of (internal and external) environmental impositions (stressors). The inherent assumption, therefore, is that self-preservation is a major selection pressure shaping the organism's regulatory processes and responses to environmental contingencies. When the organism's ability to meet this objective is perceived as being compromised, the organism is regarded as failing to cope and its welfare as being impaired (Figure 2).

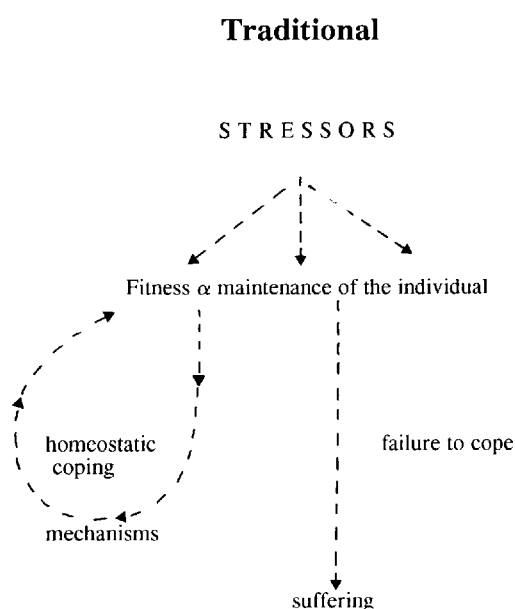


Figure 2 The relationship between fitness, self-preservation and suffering in the traditional stress/coping approach to animal welfare. Fitness is proportional to the survival and maintenance of the individual. See text.

Welfare and adaptive expendability

The argument against individual preservationism does not, of course, rule out self-preservation as an important component of most life history strategies; survival and competitiveness, even if only for a short pre-reproductive period, are likely to be important determinants of reproductive success. The adaptive expendability argument, however, sees

fitness as a property of alleles coding for strategies of expenditure of the individual (through its responses to contingencies), and the degree of maintenance and preservation of the individual is traded off against the reproductive opportunities afforded by alternative strategies of expenditure (Figure 3).

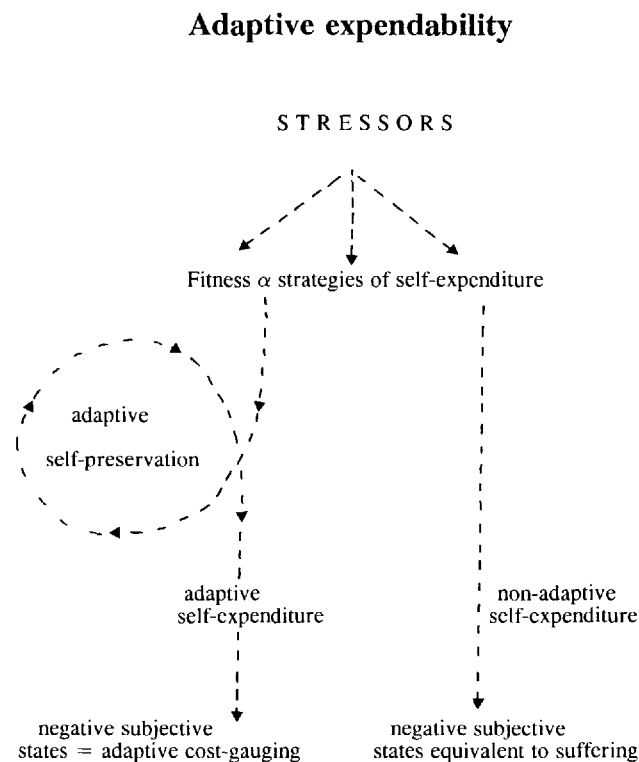


Figure 3 The relationship between fitness, self-preservation and suffering-like states in the adaptive expendability approach to animal welfare. Fitness is a property of alleles coding for life history traits and is proportional to the efficacy of strategies of self-expenditure in the current environment. See text.

Unlike the traditional 'coping' scenario in Figure 2, negative functional and subjective consequences for individual preservation can arise in two ways: a) via adaptive expenditure of self, in which any negative subjective experiences reflect adaptive cost-gauging (eg degree of fatigue as a guide to energy expenditure, degree of pain as a guide to injuries sustained in competition), and b) as a result of non-adaptive expenditure (eg frustrated hunting in a depleted environment, failed attempt to defend offspring, mounting an inappropriate immune response against a novel parasite), in which any negative subjective experiences (eg alarm, fear, anxiety, depression) reflect the inappropriateness of the organism's circumstances. Scenario (b) embraces the relationship between negative subjective states and canonical cost in Figure 1 and it is therefore here that, if the organism is capable of it at all, suffering or an analogous state is a meaningful concept. However, any cost and negative subjective

experience incurred in this fashion must be distinguished from those incurred under (a). In the case of (a) we have no reason to regard negative subjective experience as suffering-like even if the intensity of the experience exceeds anything falling into category (b). We return to this point later.

Individual preservation versus adaptive expenditure

The distinction between the scenarios in Figures 2 and 3 amounts to more than just a careful recasting of terms; the consequences of the two scenarios for the measurement and management of welfare are entirely different (Table 2). In the traditional view (Table 2a), fitness is a property of individuals and coping is a homeostatic mechanism preserving the integrity of the individual. The organism's priority is to preserve itself, so welfare management policies aim to conserve the individual and reduce pressure on its coping mechanisms. Evidence of pressure on coping mechanisms (stress) is sought by monitoring one or more of what are regarded as stress responses (see above). We can characterize this as the 'Ferrari in the garage' approach because it is analogous to a proud car owner who keeps his car in the garage meticulously maintaining the engine and polishing the bodywork. The physical and functional integrity of the car is preserved immaculately, but languishing in a garage is not what the car is designed to do. In the adaptive expendability view (Table 2b), on the other hand, fitness is a property of alleles for alternative strategies of life history investment so that any notion of coping reflects optimization of self-expenditure within the organism's overall life history strategy. The organism's priority is to maximize reproductive success by efficient self-expenditure. Good welfare management policies should therefore strive to maintain natural or acclimatized (see below) strategies of self-expenditure. Reliance on traditional measures of stress response to assess coping is inappropriate, since any apparently deleterious response can be evaluated only in the context of what is understood about the organism's adaptive strategy of self-expenditure and the impact of current circumstances on it. A good example is the relationship between social behaviour, serum corticosterone concentration and disease resistance in laboratory mice (*Mus musculus*) (Barnard *et al* 1993, 1994). After a period of social grouping with previously unfamiliar individuals, both high and low ranking males in single sex groups of CFLP strain mice show elevated levels of corticosterone, widely regarded as an immunodepressive, stress-related hormone (eg Bishop & Chevins 1988; Manser 1992). Both rank categories also show a negative relationship between corticosterone level prior to infection with a protozoan blood parasite *Babesia microti*, and subsequent resistance to the disease (Barnard *et al* 1994). In the case of low ranking males, the relationship can be interpreted in terms of frustrated escape responses in a confined environment; in the case of high rankers, however, it can be interpreted in terms of adaptive sacrifice of immunocompetence for short-term competitive edge and reproductive gain. Therefore, although both rank categories show the same clinical relationships, welfare concerns may arise only in the case of low rankers since high rankers can be argued to be showing adaptive self-expenditure in the sense referred to above. By comparison with the view in Table 2a, we can think of adaptive self-expenditure as the 'Ferrari on the road' approach, since negative effects on the organism are evaluated against the benefits of the causative response in terms of the organism's expenditure strategy.

Table 2 The implications of a) the traditional and b) the adaptive expendability approaches in Figures 2 and 3 for welfare management policy. See text.

a) Traditional	b) Adaptive expendability
Fitness is a property of individuals	Fitness is a property of alleles for alternative strategies of self-expenditure
Coping = homeostatic maintenance of the individual to ensure reproduction	Coping = optimizing expenditure of the individual within its overall life history strategy
The organism's priority is to preserve itself	The organism's priority is to maximize reproductive success through efficient self-expenditure
Good welfare management policy conserves the individual and reduces pressure on its coping mechanisms	Good welfare management policy allows natural or acclimatized strategies of self-expenditure

While the adaptive expendability approach is arguably the most appropriate, it must be adopted with care if gross misjudgments are to be avoided. To return to the example of the mice and resistance to disease above, it could be argued that the corticosterone response and reduced resistance of high ranking males was also a consequence of their captive conditions, and not an expression of natural self-expenditure at all. If confinement meant that high rankers had to fight harder to maintain status and access to resources than they would in their EEA, all we may be measuring is the inflated price high rankers are forced to pay to achieve these outcomes under inappropriate conditions. This possibility must therefore be excluded before we can accept the previous interpretation, a task that requires a detailed understanding of the evolutionary history, adaptive plasticity and mechanisms of decision-making of house mice and their artificially selected laboratory strains (see later). Once we have made the effort, however, physiological, pathological and other criteria (eg Table 1) can be used with some justification to measure the *degree* of imposition on the animal.

A second reaction to the 'Ferrari on the road' approach might be that it implies the inclusion of 'negative' elements of the organism's natural existence, such as predators and parasites, in any maintenance regime. After all, these impose major selection pressures on the life histories and activities of most organisms so, logically, they must be incorporated. Shrinking from this conclusion surely pitches us back into emotional anthropomorphism. This fundamentally misconstrues the approach. The important factor is the *selection pressure* exerted by an agent (predator, parasite, competitor etc) and its consequences for the evolution of the organism's life history strategy and rules of prioritization. As in the example of the migratory bird, if an organism is designed to respond *as if* a particular selection pressure was acting, the presence of the selection agent itself may be irrelevant. Thus, for instance, many species of small rodent remain nocturnal and seek shelter in the absence of overt predation pressure. Their circumstances should therefore cater for such 'as if' anti-predator responses. However, the likelihood of 'as if' responses depends on the extent to which the organism's responses are developmentally fixed, or acquired through experience and adaptive plasticity (again, see later).

The adaptive self-expenditure argument also highlights one of several anthropomorphic chinks in the 'normality of opportunity' stance. While the intention behind 'normality of opportunity' arguments may be to take account of the animal's evolutionary environment in determining acceptable maintenance policy, these are often predicated on subjective feelings that natural is somehow 'right' and 'free' (see Dawkins 1980) and thus preferable to captivity and constraint. Levels of activity or the extent of an animal's behavioural repertoire then become measures of freedom and opportunity and thus of welfare (see later). As Dawkins (1980, 1988) has pointed out at length, however, there are several flaws in the assumption that what is natural is also desirable. Not the least of these is that 'naturalness' is a uselessly vague concept unless we understand how organisms are designed to use it. The contrast between naturally selected strategies of self-expenditure and the objective of maintaining individual well-being, further undermines its uncritical use as a basis for welfare considerations.

Procedural alternatives and the special state of suffering

Finally, as indicated above, there is the problem of procedural interpretation and the redundancy of putative negative subjective states. As McFarland (1989) has pointed out, the concept of negative subjective states is not necessary to account for, nor are such states necessarily a consequence of, naturally selected responses to circumstance. Such responses can always be interpreted as the outcome of adaptive procedural rules that are either hard-wired (ie developmentally fixed, Dawkins 1986) or quickly acquired through learning (McFarland 1989). On this basis, therefore, the only circumstances in which a special state we might want to compare with suffering becomes likely are those outside the competence of the animal's procedural rules (McFarland 1989). Suffering or its analogue is thus viewed as an unpleasant generalized subjective state that is instrumental in the attempted avoidance of deleterious circumstances, for which the organism has no specific procedural rules of response. Panic is a good example. In humans, panic is an unpleasant and extreme subjective state that can arise in situations of crisis and may combine several extreme negative emotions such as terror and despair. Frequently the upshot is some form of precipitate action which may be frenzied and irrational but which has some chance of extricating the individual from the crisis where reasoned action has failed or been unavailable. Pain, where it is not adaptively self-inflicted (eg by continuing to fight for a valuable territory regardless of injury), can have a similar galvanizing effect. The important point is that a suffering-like state (such as panic and some states of pain) informs the organism in a general way that it is in inappropriate circumstances (the organism enters a 'state of emergency'), but does not itself provide the organism with a specific mechanism for getting out of them. Such a state is thus no less adaptive than naturally selected procedural rules or subjective proximate mechanisms; the crucial distinction is that the latter two trigger specific adaptive responses, which in the case of subjective proximate mechanisms removes the negative subjective state. Thus the rabbit alarmed by a fox ceases to be alarmed when the escape response set in train has been successful. Similarly, the chimpanzee ceases to experience pain in its jaw when it stops biting on a nut that is too hard to crack. The state of emergency we call or liken to suffering, on the other hand, exists precisely because the organism cannot trigger a ready-made specific response that will end it. Associations between the violation of an organism's evolved capabilities and negative subjective experience have also been proposed by other authors, notably Markowitz (1982) and Rollin (1989), the latter reviving the notion

of *telos* to characterize the unique, evolutionarily-determined set of 'needs and interests' of different organisms (Rollin 1981, 1989).

So far, then, we have argued that traditional approaches to studying welfare are suffused with anthropomorphic assumptions and handicapped by attempts to identify and measure suffering without regard to the functional significance of costs to the individual. While a potential for suffering-like states in other species must be acknowledged, so must the confounding effects of adaptive self-expenditure and the possibility of alien and unrecognizable analogues of suffering which are in danger of being overlooked. Key concepts in current approaches, such as fitness and coping, fall into the trap of individual preservationism, an anthropomorphic emphasis on the integrity of the individual as a priority in decision-making. If these established criteria are to be replaced with a philosophy of adaptive self-expenditure, however, what assumptions and practical implications follow?

The redundancy of measuring suffering and a working definition of welfare

It is clear that, while having some intuitive appeal, anthropomorphic criteria of welfare are undermined by careful evolutionary considerations and cannot be used as a general basis for giving benefit of the doubt. Since the measurement of suffering and well-being can also be regarded as anthropomorphic pursuits, suffering and well-being *per se* become inappropriate as general yardsticks of welfare. However, suffering is anthropomorphic only because it is a subjective state we appear to experience and then generalize to other species which may have wholly different subjective experiences or no capacity for subjective experience at all. Exposure to deleterious circumstances is not itself anthropomorphic so can still form the basis for giving benefit of the doubt, regardless of the existence or nature of its subjective experiential consequences. But what do we mean by deleterious circumstances when we acknowledge that organisms may be designed to bear costs to their well-being and survivorship?

The answer rests on the assumption that organisms are designed to function within a particular range of circumstances defined by the organisms' EEA. Within the range, the rate and degree of self-expenditure is traded off against reproductive success and is thus adaptive. Deleterious circumstances are those outside the range so that the trade-off breaks down, either because expenditure is excessive or unproductive or because normally productive expenditure is prevented or frustrated in its outcome. Here, the organism enters states for which selection has not equipped it. As an analogy we can return to our example of a domestic car. Like any machine, each of the car's systems is designed to perform within a specified range of circumstances: the engine within certain rates of revolution and internal temperatures, the suspension under certain loadings and road conditions and so on. These define the vehicle's performance criteria and differ according to the model and its performance requirements. The performance criteria in turn determine the rules of operation of the vehicle's systems – temperature modulation, fuel feed control, lubricant circulation and so on. Within these specified ranges, the components of the vehicle are expected to wear out, but at a rate commensurate with its anticipated commercial lifespan and governed to that end by its rules of operation. Forcing the car to perform outside the range of its performance criteria – eg thrashing its engine on a racing circuit or driving it over rough terrain – overrides its rules of operation and risks accelerated wear and ultimately catastrophic breakdown. By analogy, the performance criteria of organisms are the operational ranges of

its anatomical and physiological systems, the expendability of which is determined by its consequences for reproduction in the organism's EEA. These determine the organism's physiological and behavioural rules of operation (decision rules), which are thus selected to maximize reproductive potential (minimize canonical cost) within the constraint of the organism's operational limits. Although operational limits are unlikely to be known in particular cases, inferences can be drawn about them from the organism's observable decision rules and what they imply about its priorities (see below). Since we have argued (Figure 3 and discussion of procedural explanations) that suffering or analogous subjective states, if they exist in other organisms, are most likely when organisms are forced to perform outside their naturally selected performance criteria, corruption or frustration of an organism's decision rules can be used to diagnose such circumstances. In many circumstances of welfare concern, infringements are apparent from the outset. Thus a restrained animal writhing on a hotplate to test for analgesia or struggling in vain to avoid injection can reasonably be considered *a priori* to be operating outside the competence of its decision rules. In many other situations, however, such as imposed housing conditions or feeding regimes, the impact on an organism's decision rules are likely to be considerably less obvious. We shall return to the role of decision rules in diagnosing welfare problems later. First, however, we must refine slightly our concept of naturally selected performance criteria.

Performance criteria and acclimatization

Although some degree of analogy can be drawn between the design of vehicles and organisms, the analogy clearly has limits. One that is essential to welfare considerations is the ability of organisms sometimes to adapt their performance criteria to altered circumstances through physiological (eg moulting, enzyme modulation) or behavioural (eg learning) changes. Through these changes, we can regard the organism as becoming *acclimatized* (the term is thus used in a broader sense than its more traditional physiological meaning) to its new circumstances, so that its previous characteristics are no longer appropriate as a basis for judging the impact of environmental contingencies (eg Houston & McFarland 1980). Strictly speaking, therefore, we should refer to the impact of circumstances in terms of departure from acclimatized states of naturally selected performance criteria. This adaptability is itself a naturally selected design feature of the organism, extending within limits the range of circumstances under which it can survive and function. A problem at the empirical level, of course, is to distinguish changes indicating acclimatization from those that indicate disturbance to the functioning of the organism.

Acclimatization and artificial selection

Acclimatization involving adaptive plasticity must also be distinguished from that apparently brought about artificially by selective breeding. Artificial selection for phenotypic traits can shape the characteristics of organisms to new circumstances, but the analogy with adaptive plasticity is entirely superficial and artificially selected traits are problematic from a welfare standpoint. There are two interrelated reasons for this: first, artificially selected traits are chosen on the basis of preconceived, external, and often anthropomorphic or commercial/utilitarian perceptions of desirability and are likely to bear little relation to the outcome of natural selection in the same circumstances; second, the subjective experiential correlates of artificially selected traits are unlikely to be known; thus lines selected for

docility, say, may exhibit that trait because their desire for activity is reduced or because they are chronically depressed or even in pain – subjective experiences that may be unobservable externally even by indirect means. Similar uncertainties arise about the subjective correlates of other artificially selected traits such as extremes of aggressiveness. Unlike natural selection, in which associated subjective experiences are 'visible' to the selection process (through competition with alternative causes of the favoured trait that have different associated experiences, thus affecting survival and function in different ways), artificial selection works crudely on limited phenotypic characters and does not integrate traits into adaptive suites. This is evident, for example, in the lack of intercorrelation across strains between artificially selected changes in focal behavioural traits and changes in the performance of other activities, often closely related functionally (Brain 1989). As a result, while artificial selection can undoubtedly change the performance criteria of an organism, there is no basis for supposing the changes *adapt* the organism to its circumstances or that the environment in which artificial selection has taken place is equivalent to an EEA. The fact that artificially selected lines retain vestiges of their evolutionary past does not mean that comparison with presumed function in the EEA is appropriate, it simply means the distortions of artificial selection have not changed everything. The use of artificial selection to manipulate traits, especially behaviour, thus has alarming possibilities for the invisible subjective experiences of the organisms in question.

Performance criteria and a definition of welfare

As Broom and Johnson (1993) have emphasized, a definition of welfare is required for scientific study, for other practical purposes and for legislation. Moreover, it must fulfil a number of requirements to be workable. Following Broom and Johnson, therefore, a useful definition must a) refer to a characteristic of an individual which is measurable, b) use measures that are independent of moral judgments about welfare (even though moral judgments are responsible for concern about welfare in the first place) and c) use measures that vary over a range and are thus quantifiable rather than being all-or-nothing dichotomies (such variation, Broom & Johnson argue, is inherent in the colloquial use of the term 'welfare' and in its original use to denote how well an individual 'fares' or 'travels through life'). While we agree with Broom and Johnson that these are essential criteria for a useful definition of welfare, we disagree with them that the traditional concepts of coping, stress and suffering represent a helpful application of them. Instead we argue that measures of departure from acclimatized performance criteria should be the basis for defining impact on welfare. Such a definition fulfils all three of Broom and Johnson's (1993) requirements and is robust to all the objections to existing approaches to welfare set out above in that it a) allows objective definition and measurement of circumstances that are inappropriate for the organism, b) is robust to procedural objections, c) takes account of the adaptive self-expenditure of the organism, d) removes the stumbling block of defining and testing for a subjective state (suffering) that is inaccessible by any direct means and e) removes reliance on evidence of pathology or physical or functional impairment to infer compromised welfare.

Defining welfare in this way also emphasizes the interaction between welfare considerations and the scientific value of procedures involving organisms, with all the commercial/applied implications that follow. In the well-known 'Bateson cube' trade-off (Bateson 1986), the scientific value of research (eg medical application, technological advance or simply enhanced understanding) is pitted against its consequences for suffering

in the organism concerned. Thus a greater degree of suffering might be tolerated in the pursuit of especially valuable results. Implicit in this model is the assumption that suffering and scientific value are independent of each other. Suffering may arise as a result of an experimental procedure but it does not itself influence the scientific value of the outcome; the value is a given which is weighed against the apparent degree of suffering imposed in judging the moral justification for the study. While qualitative arguments along the lines of 'unhappy animals cannot be functioning normally' have often been levelled at this implicit independence, they suffer from the subjective arbitrariness and untestability that we have highlighted above. However, defining welfare in the terms we propose renders the interaction between suffering and scientific value explicit, since circumstances in which suffering-like states are likely are defined as those outside the range in which the organism is designed to function. Regardless of ethical arguments, therefore, welfare concerns in the sense of appreciating the degree of appropriateness of the organism's circumstances should be a priority purely from a scientific standpoint. While it can be argued that there are situations in which welfare is irrelevant to scientific value (eg simply using a living organism as a source of a biologically active chemical such as a hormone or enzyme), good welfare is likely to be essential where the integrated functioning of the organism is involved (as in most physiological, pharmacological and behavioural contexts) and impairment of function must be acknowledged as a constraint of the study design in evaluating results. Good science and good welfare therefore go hand in hand not because of the putative complications of 'unhappiness' but because acknowledgment of design is inherent in both.

We have now made a case for basing measures of welfare on what an organism is designed to do rather than on any anthropomorphic criteria. We have suggested that studying the behavioural and physiological decision rules of other species provides the most reliable approach to giving the benefit of the doubt, because it is independent of assumptions about the nature of subjective states and robust to all the perennial objections to other measures of welfare. However, the approach requires a considerable investment in understanding the nature of decision rules and the environments in which they were designed to operate, and we have not yet indicated how it can be put into effect in practical terms.

Measuring performance criteria

It is easy to talk in a hand-waving way about naturally selected performance criteria, but proposed yardsticks of welfare are no use unless they lead to practicable measurements. How, then, are we to assess performance criteria and measure departures from them in real organisms?

Since welfare is concerned with the impact of circumstances on an organism's ability to function (hence the historical emphasis on coping), measures of welfare impairment must be in terms of the appropriateness of the organism's performance criteria in the face of such circumstances. As argued above, we can use the organism's observable decision rules to gauge infringements of its performance criteria. Decision rules can be grouped into two categories: first, *rules of time and energy budgeting* which determine how the organism prioritizes expenditure of its limited time and metabolic resources across life history components and activities; and second, *rules of response* which determine how it reacts behaviourally and physiologically to environmental contingencies (eg mating opportunity, presence of a predator, infection, temperature change, poisoning). Of course, there is an

interaction between these categories; for example, if a predator suddenly appears, the organism's rules of time and energy budgeting allocate a high priority to escape behaviour, but the form of escape (bolting down a hole, fleeing, freezing etc) is determined by its rules of response. In addition, both sets of rules are likely to be modulated by phenotype-limited factors such as body size, immunocompetence, learning ability, sensory acuity and so on. Identifying decision rules and measuring their competence in given situations, however, begs a number of important questions:

- 1 What are the selection pressures shaping the decision rules in the organism's EEA?
- 2 How do the rules adapt the organism to these selection pressures?
- 3 How do current circumstances differ from those prevailing in the organism's EEA?
- 4 How do these differences affect the expression and efficacy of the organism's decision rules?

Providing answers to these questions requires a detailed appreciation of the organism's evolutionary ecology but also, since decision rules are likely to be noisy approximations of optimal decisions (eg Barnard 1984; Stephens & Krebs 1986), the proximate mechanisms by which the rules lead to priorities and responses. From a welfare perspective, therefore, comparisons between current circumstances and the EEA depend not on analogies at the level of environmental structure but on how any differences at this level are interpreted through more or less coarse-grained decision rules. To take a simple example, if individuals of an insect species use the rule 'orientate towards anywhere dark' to escape a predator then it probably makes no difference to the insect's perception of a satisfactory outcome whether the source of darkness is a rock crevice or a discarded cigarette packet; the fact that it usually ends up in a rock crevice in its natural environment does not mean a cigarette packet is not a perfectly appropriate substitute in a captive environment. If, on the other hand, the insect uses an environmentally specific rule such as 'follow the lemony odour gradient deep into this flower', the provision of anything but the correct plant species is likely to be unsuccessful. Again, therefore, the environment-general expression of decision rules (Table 1) is emphasized; the organism always operates according to its decision rules and the appropriateness of the environment is determined by its accommodation of the rules. This means the mechanisms underlying the decision rules, not simply the functional outcome of the rules. Altering an organism's environment without appreciating the decision rules by which the organism operates risks unpredictable consequences for welfare. In an applied context, this has serious implications for so-called 'environmental enrichment' programmes where organisms' environments are often manipulated on the basis of anthropomorphic notions of diversity, complexity and novelty, or apparent natural relevance, without appreciating the perception and functional significance of such manipulations from the organism's viewpoint (eg Rupniak & Iverson 1989; Chamove 1989; McGregor & Ayling 1990; McGregor *et al* 1991).

Since welfare considerations must be based on an organism's naturally selected, acclimatized performance criteria, it is obvious that the implications for welfare of any given set of circumstances will be specific to the organism concerned. Moreover, since decision rules will be influenced by phenotype-limited characteristics such as body size, health and experience, welfare implications will also vary between individuals of the same species. Despite this, however, we can identify the types of constraint on decision rules that are likely to lead to impairment of welfare.

Rules of time and energy budgeting

The work of McFarland (eg McFarland & Houston 1981; McFarland 1989) provides the clearest and most helpful analysis of time budgeting and prioritization and its relevance to welfare, and we adhere closely to the concepts and approach developed there. We envisage three categories of constraint on time and energy budgeting that have implications for welfare as we have defined it.

Resilience and squashing

The first concerns the well-established concept of resilience. From a behavioural viewpoint, it has long been argued that patterns of time and energy budgeting reflect the relative importance of different activities in the repertoire in terms of the individual's reproductive potential (eg Caraco 1979a, b; Houston & McFarland 1980; McFarland & Houston 1981; Shaffery *et al* 1985; Dawkins 1988). The importance of an activity thus reflects the consequences of its outcome (eg acquiring a resource) for reproduction. When the time and energy to be distributed across activities becomes constrained, allocation to important activities is conserved at the expense of less important activities. By analogy with economic demand theory (Lea 1978), important activities are thus said to be 'resilient' (and demand for their outcome 'inelastic') while less important activities are 'squashable' (and demand for their outcome 'elastic'). The severity of a constraint on budgeting rules can therefore in principle be measured in terms of the squashability of the activities lost from or reduced in the repertoire. Severity is greatest when normally resilient behaviours become squashed. However, constraint must be measured against repertoires pertaining to the organism's EEA, taking account of phenotype-limited differences in, and adaptive plasticity (acclimatization) of, priorities. Thus constraints imposed by the environment may squash behaviours within the repertoire, or even remove them altogether, but such changes cannot be assumed *a priori* to reflect constraint without understanding individual differences in priorities and effects of acclimatization. In some cases organisms may budget their time to minimize energy expenditure so that as much time as possible is spent sitting around doing nothing (Pyke 1979; Herbers 1981). There is thus no basis for predicating welfare judgments on simple comparisons between the amount of time spent active or the number and/or types of behaviours in the repertoires of captive and free-living individuals (Thorpe 1965; Martin 1975). Indeed, a lot of activity or a large repertoire may be serious negative indicators of welfare (Hurst *et al* in press). While behavioural resilience can be used to infer priorities and strength of demand, demand can also be assessed independently by means of preference tests or manipulating the cost of achieving a priority outcome (Table 1, see also below). However, as Dawkins (1988) has pointed out, these kinds of test require the same attention to the organism's perception of its environment and decision rules if they are to provide results of any value. This may involve complex and subtle attributes such as the organism's perception of available alternatives, its perception of the degree of openness of its current environment and the time horizon of its rules of prioritization (Lea & Roper 1977; Hursh 1984; Houston & McNamara 1988; Dawkins 1988).

Distortion of priorities

Budgetary rules may be constrained other than by the imposition of time and energy constraints. Exposure to inappropriate environments may shift priorities within the repertoire so that certain behaviours occupy a disproportionate amount of time. Thus a confined animal

may spend most of its time attempting to escape or remain out of view at the expense of other, normally high priority, behaviours like sleeping or foraging. Such changes differ from acclimatization in that they do not represent adaptive accommodation of the opportunities and constraints inherent in the organism's current circumstances. An example of an acclimatized shift in relative priorities would be the tendency to spend more time in behaviour A, say resting, rather than switch to behaviour B, say feeding, because the cost of switching from A to B has been increased, perhaps by the introduction of competitors. The presence of competition, and thus risk of aggression and injury, raises the canonical cost of food deprivation at which it pays the organism to change behaviour (see Larkin & McFarland 1978), so the delay in switching represents an adaptive shift in time and energy allocation and is within the competence of the organism's decision rule. The shift becomes maladaptive distortion when the switch is delayed beyond the acclimatized cost threshold, for instance because superior competitors physically prevent access to the food and thus remove control of prioritization from the individual concerned.

'Limbo'

Changes in time and energy budgets may occur because the environment does not facilitate or necessitate the expression of what would normally be the current priority behaviour. This may be because a resource which is usually acquired as the outcome of a particular behaviour is already provided and the need for the behaviour consequently removed. However, the welfare implications of providing resources once again depend on the organism's decision rule. If the rule instigates behaviour in response to perceived resource availability then artificially providing the resource may lower the priority for performing the behaviour, an example being the effect of providing nest material on the tendency for domestic sows (*Sus scrofa*) to seek it out (Baxter 1983). If, on the other hand, the rule instigates behaviour regardless of artificially provided resource, as in the earlier example of the caged migratory bird, the priority remains and the behaviour is expressed without the appropriate outcome (see below). Provision of resources or other requirements in captive environments may lead to a general state of the organism which McFarland (1989) refers to as *'limbo'*. As McFarland (1989) puts it, an organism that has to spend less than the usual amount of time obtaining food, water, shelter and other vital requirements effectively has time and energy to spare. In the free-living state, these would normally be spent on next-in-priority activities, say looking for a mate or patrolling a territory boundary. But if the current environment does not provide the opportunity for these, the organism enters a state of *'limbo'* with which its decision rules have not been designed to deal and in which it is effectively paralysed by lack of options. *'Limbo'*, however, must be distinguished from situations in which lack of opportunity frustrates a priority activity but the organism is able to switch to a lower priority activity, even if that is inertia (as, for instance, when a replete dominant individual which would normally defend nest and food sites is unable to do so because of the inappropriate structure of its environment, so conserves energy by sleeping instead).

Rules of response

While lack of opportunity and other constraints imposed by the environment may frustrate or distort prioritization, they are also likely to impact on the organism's rules of response. Again, we can envisage a number of categories of effect with implications for welfare:

Frustration

Lack of opportunity may frustrate decisions both at the level of expressing current priority (budgeting rule, see above) and at the level of performing the behaviour appropriate to the priority (response rule). For example, if a hungry animal is presented with food in an inappropriate fashion, say in a novel container it does not recognize as a source of food, the animal may simply switch to its next-in-priority behaviour so that feeding is not expressed at all, or it may attempt to feed using its normal technique and fail. Failure may result in a distortion of the animal's time and energy budget because the animal persists in its fruitless effort (thus highlighting the interaction between the two classes of decision rule), but the cause is frustration of the rule of response rather than the rule of prioritization. An example of frustration that is likely to be widespread in captive environments is that of escape responses to attack among subordinate individuals, where groups are maintained in a confined space and the opportunity for avoidance limited.

Inappropriate outcome

In other situations, the organism may achieve an outcome from its response, but the outcome is inappropriate in some way. Inappropriateness here may be difficult to recognize if it is gauged simply on the fact that the organism shows an expected response towards something rather than on the functional significance of the outcome. For instance, it is easy to imprint the young of various species on artificial objects (eg Hess 1973; Bateson 1979) because the rule of response leading to attachment works crudely (it did not evolve in an environment where mistaken attachment to balloons, matchboxes or soft toys was a problem). While the individuals concerned readily form such attachments, however, these cannot fulfil the functional requirements for which the imprinting rule was designed. The designed outcome of the attachment is thus frustrated. On the other hand, a dog chasing a ball is also responding to an artificial stimulus, but in this case the response may reflect play which is a natural element of the behavioural repertoire of dogs and an appropriate outcome in itself. Chasing a ball is thus less likely to constitute a response rule infringement in dogs than is imprinting on a balloon in chicks. However, we should need to understand the function of play (Martin & Caro 1985) and the appropriateness of ball-chasing in this context before being certain. In other cases, inappropriate outcomes arise from corruption of salient cues in the environment. House mice (*Mus musculus*), for example, use urinary odour cues on the substrate as a template for the membership and social structure of their group (Hurst 1993; Hurst *et al* 1993). Responses to encountered individuals, especially dominants, are then determined by the match between their individual odour and those in the template. Disruption of substrate odour cues, eg by cage cleaning in captive environments, can in turn disrupt the outcome of social encounters by corrupting the template on which the matching rule is based (Gray & Hurst 1995).

'Purgatory'

Finally, rules of response may instigate behaviour appropriately but be overwhelmed by the magnitude of the environmental imposition. Under these conditions we can envisage an organism entering a state of '*purgatory*' in which its only available, and normally effective, response is inadequate to achieve the appropriate outcome (note that this broadens McFarland's (1989) use of '*purgatory*' which he restricts to physiological states approaching the organism's lethal limits). A simple example would be the overwhelming of panting as

a cooling response by exposure of the organism to excessively high temperatures. Panting is the right response, and is normally effective in regulating body temperature, but the excessive ambient temperature is outside its range of competence. The disruption of substrate odour cues in the mouse example above, might also lead to 'purgatory' in individuals in which responses that normally settle and maintain social relationships become ineffective so that groups enter a state of persistent social flux. Interestingly, the risk of this is greater when cages are cleaned only partially (distorting the relative predominance of dominant versus subdominant/subordinate odours) rather than completely (removing odours altogether) (Gray & Hurst 1995). 'Purgatory' by persistent social disruption may also be induced by housing mice at high densities, where the inability of high ranking males to maintain dominance increases aggression among subordinates and results in a high turnover of dominants (Poole & Morgan 1973).

Radishes versus chimpanzees: priorities for welfare

An obvious implication of the argument developed here is that it applies to all organisms regardless of taxonomic level. In principle, therefore, the radish plant in the garden seems due the same welfare consideration as the chimpanzee confined in a zoo. Objections to such blanket inclusion are generally based on comparisons of organizational complexity and assumptions about the capacity for sentience and thus suffering (see Duncan's (1993) 'pine tree argument'), yardsticks that make anthropomorphic bias almost inevitable. We make no apology for our all-embracing criterion, however. All organisms are designed to survive and reproduce. Their anatomical and physiological systems are thus designed to ensure these outcomes within the limits of their acclimatized performance criteria. The life history strategies of all organisms, therefore, are subject to resource budgeting constraints and environmental contingencies with which their decision rules are designed to deal. While our earlier examples have considered mainly behavioural decision rules, the impositions we discussed apply to all forms of decision rule: behavioural, physiological, developmental and so on. The potential for constraint on decision rules, and thus for mechanisms of registering constraint (all be they species-specific), is universal. The objection that welfare implications of such constraints are meaningless in the absence of human-like sentience and suffering (eg Duncan 1993) does not bear close consideration. Apart from the problem of arbitrary anthropomorphism, the evolution of sentience and psychology as an emergent property of physiology is likely to have produced a phylogenetic continuum (eg Dennett 1991) in which definitional thresholds are a nonsense.

However, this does not mean that our intuitive concern (Kennedy 1992) for animals over plants and 'higher' organisms over those 'lower' down on the phylogenetic scale is misplaced. But instead of being based on degree of similarity with ourselves or hypothetical thresholds of mental function, the reasons emerge from differences in life history strategy and the nature of decision rules and their implications for the impact of environmental circumstances on performance criteria.

Life history strategies

From the welfare argument developed here, the key difference between animals and plants is not that plants lack the neural organization for sentience and suffering (or other characteristics of anthropomorphic significance), but that individual plants are generally not

designed to respond to inappropriate circumstances by avoiding them and seeking out something more suitable. While plants can undoubtedly be subjected to circumstances that infringe their performance criteria and decision rules, it seems unlikely that selection will have equipped them with the subjective experiences or procedural rules which in animals are designed to remove them from such circumstances. By the same token, the selection pressure for a generalized subjective 'state of emergency' that might be labelled 'suffering' seems likely to be weak. However, we must still exercise caution here. Many plant species *can* respond to adverse conditions in ways that effect some sort of escape, for instance through solar tracking and vegetative dispersal strategies (Harper 1977). Frustration of these strategies (eg by removing stolons, suckers etc) may constrain the plant to remain in what it perceives as deleterious circumstances (eg adverse soil pH, nutrient deficiency, shade) or frustrate its competitive strategy of 'space capture' (Harper 1977; Charnov 1984). Moreover, precisely because 'behavioural' options for changing circumstances are limited, plants may rely on sophisticated physiological accommodatory responses (eg Gresshoff 1993; Wilkinson 1994) the frustration of which is likely to be difficult both to detect and to evaluate in terms of impact. Dismissing the potential welfare implications of this simply because the organism is a plant is difficult to justify objectively, even though the likelihood that such responses reflect blind procedural rules without subjective feedback of the outcome is considerably increased. As we have stressed, our emphasis on constraints on decision rules as yardsticks of welfare seeks to provide an achievable objective measure which is independent of taxonomic level and anthropomorphic empathy. However, there is no implication that all organisms *do* suffer if their decision rules are infringed, merely that infringement is the only objective way of identifying when they might. Decisions as to whether particular organisms do or do not suffer can be predicated only on estimates of the adaptive value of such a state given the organism's life history and the nature of its decision rules. We have argued that there are life history reasons for believing that plants are less likely than animals to have evolved states of suffering, but there are clearly situations in which, on present understanding at least, such states cannot be ruled out *a priori*.

Our intuitive feeling that higher vertebrates, especially mammals, generally deserve greater welfare concern may also be justifiable from a life history viewpoint. Many species of vertebrate are relatively long-lived and many invest heavily in parental care, which means that the preservation and maintenance of the individual are likely to be high priority components of life history strategies. As a result, circumstances that impact on maintenance and survivorship are likely to reflect a degree of constraint on decision rules that risk experiences akin to suffering. However, this interpretation will vary with species, being plausible in long-lived elephants for example, but more questionable in short-lived, high turnover, small rodents.

Complexity

While the temptation to treat more complex organisms with anthropomorphic empathy must be resisted, increasing complexity undeniably brings with it greater scope and sophistication at many levels: sensory perception, information processing, learning, emotion, motor skills and so on. Such increased capacity may have several consequences from a welfare viewpoint.

First, greater sensory and information capacity may increase the sensitivity with which circumstances are distinguished as desirable or aversive, thus leading to more subtle causes of aversion. Second, a number of implications arise from the evolution of flexible, experience-based, rather than developmentally fixed, decision rules.

At first sight, flexibility in decision rules seems to offer greater scope for dealing with environmental contingencies, and thus for reducing the likely welfare impact of change. However, this makes the dangerous assumption that flexibility is open-ended. Like any other aspect of decision-making, flexibility will have been designed in the organism's EEA and will therefore be geared to contingencies arising there rather than in an artificial or otherwise altered environment. The fact that adjustments in response occur in artificial environments cannot be interpreted as adaptive plasticity without appreciating the functional significance of the change in the context of the organism's performance criteria. Thus, an animal that spends most of its time in its natural environment foraging and exploring but the majority of its time in a cage inert, may be showing adaptive plasticity (its food is handed to it on a plate so it spends the extra free time conserving its energy and avoiding exposure to predators, just as it would in the wild if the constraint of foraging was lifted). Alternatively, however, it may have entered a state of 'limbo' because the cage does not provide the opportunity for the active alternatives (eg social interaction, nest maintenance) it would normally have taken up. In the first case, inertia reflects an adaptive time budget shift towards resting, in the second it reflects paralysis of the animal's system of prioritization. Such changes in response may be compounded by plasticity in the mechanisms for achieving priority outcomes and the effects of this on prioritization itself. To pursue the above example, the relative priority of two actions, say feeding and resting, may be altered by environmental circumstances if these affect the cost of performing them, eg by forcing the organism to adopt different foraging strategies. While this may reflect adaptive plasticity in prioritization, it must be distinguished from maladaptive distortion (see above). Distinctions like those between adaptive plasticity and 'limbo' or distortion are therefore likely to be considerably more difficult than identifying constraints on relatively inflexible, developmentally fixed rules (eg klinokinesis in woodlice (Isopoda, Oniscoidea) in relation to substrate moisture (Carthy 1966)).

Sophisticated, flexible decision rules may make constraints difficult to identify in another way. The more complex a machine, the more opportunity there may be for misleading 'knock-on' consequences of faults which obscure the real problem. For example, in some modern electronically-regulated car engines, a fault in the cooling system (eg a leaking radiator) may cause sensors to register a change in the conditions of fuel combustion in the engine with the effect that the automatic choke kicks in and causes the engine to hunt. The problem is initially diagnosed as a faulty choke which is duly adjusted or replaced only for the symptoms to recur. By analogy, increased exploratory behaviour and reduced food intake by subordinates in a captive group of rats may be attributed to competition for food, a conclusion reinforced by high levels of aggression observed around the food bowl. The decision is to reduce competition by providing a second food bowl. Unfortunately, this has little effect on aggression, exploration or food intake. The reason turns out to be that increased activity is not a consequence of competition for food, but of a lack of resting sites where subordinates can avoid certain high ranking males. Subordinates thus spend very little time resting or feeding and wander for long periods around the enclosure. Because space is

limited, they repeatedly encounter high ranking individuals near the food bowls and are either attacked or avoid the area around the food bowls altogether. While the behaviour of the animals has all the appearance of aggressive competition for food, this is not the cause of the increase in exploratory activity but a knock-on effect of constraints elsewhere in the environment and their impact on the rats' rules of time budget adjustment. The example also shows how the complexity/flexibility per se of behaviour can lead to welfare problems, since problems arise in this case from the ability of rats to generalize avoidance responses between different contexts. Avoidance of food thus occurs as a result of a lack of availability of resting sites and despite increased food demand due to higher levels of activity. Greater flexibility and complexity of response may thus simultaneously create more opportunity for infringement of decision rules and greater difficulty in diagnosing infringements.

Conclusions

In their recent paper, Mason & Mendl (1993) ask 'why is there no simple way of measuring animal welfare?' The question arises because of the difficulty of interpreting behavioural and physiological measures now widely agreed to reflect welfare. We argue that at least part of the problem is an inappropriate view of what welfare should mean. In order to assess the appropriateness of an organism's environment and the impact of experimental or other procedures on its welfare, we must understand what the organism is designed to do and how prevailing circumstances impinge on its functional design. This means understanding what we refer to as the organism's naturally selected performance criteria and rules of operation. While this is in keeping with previously expressed views (eg Markowitz 1982; Rollin 1989), these have not embraced the functional significance of negative subjective states in the context of adaptive life history. Inherent in our view is an acceptance that organisms are designed for self-expenditure and that the importance of the maintenance and survival of the individual varies between organisms and different life history strategies. As a result, the behavioural and physiological measures that are currently accepted as indicating poor welfare cannot be interpreted in this way without appreciating the functional significance of the apparent impairment to welfare (a parallel line of reasoning underpins the developing field of Darwinian medicine (Nesse & Williams 1994)). The traditional notions of coping and stress imply homeostatic preservation of the individual. While a degree of self-preservation is likely to be important in any life history strategy, other life history considerations may conflict with it in the pursuit of reproductive success; physical impairment or even death may thus be adaptive trade-offs favoured by selection and built in to the decision-making machinery of the organism. Blanket emphasis on homeostatic notions of coping and stress in welfare considerations can therefore be viewed as anthropomorphisms based on our own relative longevity. This is compounded by a widespread misapplication of the concept of fitness in welfare contexts. An approach to welfare such as we suggest both avoids these difficulties and removes the stumbling block of measuring subjective states because these are subsumed without need for direct measurement within the concept of design; indeed, the likelihood of the special subjective states we compare with suffering is *defined* in terms of the degree of imposition on the organism's design. Benefit of the doubt is thus automatically given.

It is important to emphasize once again that we are not suggesting other organisms do not have subjective experiences and cannot experience suffering or something like it. Neither

are we suggesting that the potential for suffering is outside the scope of scientific concern (cf van Rooijen 1981). On the contrary, as we have said, we share Dawkins's (1993) view that the subjective experiences of other species are legitimate, if still distant, targets of scientific investigation and agree with her that recent research is shedding interesting light on other mental worlds. On its own, however, this understanding is of limited use in a welfare context unless we appreciate which negative subjective states the organism willingly enters into and which are unwelcome impositions. The problem is greatly exacerbated if, as is currently the case, we are forced to rely on behavioural, physiological or other indirect measures which are several stages removed from any associated subjective state and may not even correlate with subjective states in an homologous way across species. Since interpretation of any of these kinds of measure relies on prior assumption as to their functional significance, we agree with Fraser (1995) that, at this level, '. . . there is no single measure, nor any purely objective way of combining different measures, that eliminates value-related disagreements . . .'. Until such subjective uncertainties can be overcome with some confidence, the most reliable indirect indicator of welfare problems seems to us to be the mismatch between designed and imposed performance.

Animal welfare will always be difficult to measure because it will always rely on an understanding of other species' perceptions and decision rules. However, in the absence of such understanding, behavioural, physiological and clinical measures have no context in which they can be interpreted. This is why animal welfare is currently as difficult to measure as it is. The urgent requirement, therefore, is for basic research into the behavioural ecology of decision-making and prioritization in other organisms, and how the naturally selected rules of other organisms function in the kinds of environment to which we subject them. In the light of this information, we may indeed be able to draw inferences about the degree of welfare impairment from some established measures.

Acknowledgments

We thank Marian Dawkins, Rachel Scudamore, Rosi Hare, Francis Gilbert and two anonymous referees for helpful discussion and/or comments on the manuscript and David de Pomerai, Chris West, Angela Walker and Eric Wheeldon for further fruitful discussions. The arguments in this paper developed in part as a result of work on the welfare of caged rodents generously supported by Zeneca plc and a research grant from the Home Office. JLH is also supported by an Advanced Postdoctoral Fellowship from the Biotechnology and Biological Sciences Research Council.

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