



ESSAYS

Ethical regulation and animal science: why animal behaviour is special

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Like other areas of animal science, the study of animal behaviour is becoming increasingly subject to ethical regulation and legislation. Sensible and well-informed regulation is to be welcomed both on compassionate grounds and because misuse of animals is likely to compromise the science itself. However, it is evident that much of the impetus and direction in the regulation debate is coming from one particular corner of animal science: that concerned with utilitarian and commercial interests taking place in controlled laboratory environments. This is sustained by an overemphasis on potential medical benefits as the perceived key selling point for animal science to a hostile public. Such a bias risks potentially unfortunate consequences for wider aspects of animal science, and is unlikely to serve the best welfare interests of animals when viewed from their own biological perspective. I review some of the concerns that arise from this, and suggest that the study of animal behaviour has a uniquely important role to play both in the development of animal welfare science itself and in the public debate about the regulation of animal science as a whole.

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Like many other animal scientists, we who study animal behaviour are becoming increasingly enmeshed in regulatory frameworks aimed at safeguarding the ethical propriety of our experimental and observational procedures. Institutional, professional and national and, increasingly, international governmental bodies impose near forensic scrutiny on applications for animal research and the subsequent progress of work (e.g. Hudson & Bhogal 2004; Horgan & Gavinelli 2006; Laszlo & Csaba 2006; Laurance 2006). In principle (and leaving aside the cost of the unwelcome bureaucratic consequences), this is as it should be. No scientist who is seriously interested in the behaviour of animals wishes to see them used in a cavalier and thoughtless fashion; compassionate grounds apart, such abuse would be likely to compromise the science itself (e.g. Russell & Burch 1959; Barnard & Hurst 1996; Bateson 2005). The Association for the Study of Animal Behaviour (ASAB) and its North American partner the Animal Behavior Society (ABS) have long had their own, regularly reviewed, ethical guidelines (http://www.elsevier.com/framework_products/promis_misc/ASAB2006.pdf)

through which they oversee work published in *Animal Behaviour* and presented at ASAB and ABS conferences, and both societies support fully the proper regulation of research using animals. However, at least within the U.K. and Europe, there are disquieting signs that the debate about regulation and legislation is fast becoming parochialized within one sector of animal science: that to do with broadly biomedical and commercial research. The argument I want to make here, based largely on the situation within Europe, is that this is a potentially distorting influence that is likely to have unfortunate unintended consequences for animal science in the wider sense that mainstream biologists would recognize, and, moreover, is unlikely to serve the welfare interests of animals when considered from the animals' point of view.

THE NATURE OF ETHICAL CONCERNS ABOUT ANIMAL SCIENCE

All animal science brings ethical concerns in its wake if it has an impact on the animals concerned. However, it is useful to make a distinction between two

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fundamentally different reasons for using animals. The first, which encompasses various forms of utilitarian research (e.g. Bateson 1986, 2005; Singer 1990; Reiss 1993), exploits animals as resources, and includes studies for medical, consumer commercial, pharmaceutical, toxicological, military and other purposes which confer health, social/political and/or financial benefits on human society at large. This is overtly self-interested exploitation which we justify ethically in terms of the magnitude of resulting societal benefits. Ethical concerns are given added political impetus by the pressure of public opinion (especially from the extremist animal rights wing), which is perhaps felt more acutely by the exploitative biomedical/commercial sector than by others within animal science (Berg & Hammarstrom 2006; Signal & Taylor 2006).

The second category, which I shall refer to as curiosity-driven research, uses animals to satisfy an intellectual desire to understand the world around us (e.g. Reiss 1993). It is thus no less self-interested than utilitarian research (Cuthill 2007), but simply measures the worth of studies in a different currency. Curiosity-driven research also sees good welfare as a prerequisite for good science and is subject to a measure of public pressure. The intrinsic self-interest of utilitarian and curiosity-driven research provides shaky ground on which to build a moral case for exploiting animals, and will never cut much ice with hardcore abolitionists because no amount of cost/benefit relativism will change the extreme moral view that we have no right to exploit other animals for our advantage. However, there is another argument that provides a firmer moral case for research on animals, which I refer to as a 'moral need to know'.

The Case for a 'Moral Need to Know'

That we are having a serious impact on our planetary cohabitants, whether ecologically or through managing them for food or the whims of the commodity market, is hardly in doubt (e.g. Clark et al. 2006; Kim & Byrne 2006; Mattson & Angermeier 2007). Much of that impact, whether deliberate or incidental, arises from indifference in the face of financial or wider societal benefits, but it is exacerbated by our as yet shadowy grasp of what can be done from the organisms' point of view to alleviate it (Barnard & Hurst 1996). As witting agents of the problem, and the only ones capable of planning and effecting a response to it, we can be argued to have a moral obligation to respond in a properly informed fashion. (While Cuthill 2007 argues that even studies designed to benefit animals themselves can be construed in terms of a self-satisfying altruistic 'feel good' factor, and so are also essentially self-serving, this is a criticism that can be levelled at any course of action based on moral principles and is thus an argument against ethical scruples generally rather than moral attitudes to animal science per se.) A sophisticated understanding of how other species function, and thus of their 'welfare' in the rounded sense of being able to function on their own terms — what I shall call 'evolutionarily salient welfare' (see below) — is thus essential if

the problem is not simply to be compounded by well-intentioned, but misguided, shots in the dark. Key fields of animal biology here are behavioural and population ecology, conservation biology, veterinary biology and animal welfare itself, but all aspects of whole-organism biology are likely to play an important role. Understanding in these fields cannot be gained simply by staring passively at animals in their natural state, but requires manipulative and sometimes invasive experimentation. So what do I mean by evolutionarily salient welfare?

WHAT IS WELFARE AND WHAT SHOULD IT MEAN IN PRACTICE?

There is little consensus on either what welfare really means in other species or how it should be measured (e.g. Mendl 1991; Mason & Mendl 1993; Fraser 1995; Dawkins 2006). As has been noted by several authors (e.g. Moberg 1993; Barnard & Hurst 1996; Clark et al. 1997; Skutch 1997; Timberlake 1997; Serpell 2003), traditional concepts and measures of welfare have relied on a suite of essentially anthropomorphic criteria, which owe more to how we think we might feel in the animal's circumstances than to a deep understanding of how the animal is actually likely to feel. These broadly emphasize comfort (the extent to which the animal is maintained with adequate space and basic requirements for subsistence; e.g. Wolfensohn & Lloyd 1994), health (the extent to which it is maintained hygienically and free from infection, injury, 'stress' and behavioural abnormality; e.g. Hurnik 1988; Broom 1991; Burn et al. 2006; Dawkins 2006), normality of opportunity (maintenance in circumstances that allow a perceived natural range of behaviours and provide a perceived natural social, sexual and reproductive environment; e.g. Thorpe 1965; Martin 1975; Bracke & Hopster 2006), or philosophical stances on ethics and animal rights (e.g. Rollin 1981, 1989, 1993; Midgley 1983; Regan 1984; Berg & Hammarstrom 2006), including arguments for respecting the species-specific 'dignity' of other animals (e.g. Rollin 1998; Wickins-Drazilova 2006). Such criteria form the basis of the so-called 'five freedoms' (freedom from (1) hunger and thirst, (2) discomfort, (3) pain, injury or disease, (4) fear and distress, and freedom to (5) express normal behaviour) proposed by the U.K. Farm Animal Welfare Council (Harrison 1988), and inform the ubiquitous 'three Rs' (Replacement, Refinement, Reduction) originally set out by Russell & Burch (1959) (see also Smyth 1978) and now the guiding credo of welfare regulation in the U.K. and Europe. Welfare concerns arise when infringements of these criteria are deemed sufficiently serious to risk the animal 'suffering', where 'suffering' is a putative negative subjective state that is rarely defined, either in terms of what it comprises or of where on a presumably sliding scale of negativity it lies. I shall return to this problem later.

Arguments in favour of anthropomorphic criteria include our obvious evolutionary continuity with other species, with its potential for homologous psychological responses to circumstance, at least in moderately close relatives, and the fact that our own subjective experiences provide the only model we have of 'suffering' and so,

perform, act as a 'best of a bad job' comparator. Arguments against hinge on the point that evolution is as much about adaptive specialization as it is about continuity (McFarland 1989); thus, while there may be similarities between species at a general level that may have implications for welfare (homology in central nervous and sensory system structure, physiology and cognitive processes, for example), there may be adaptive differences of far greater significance, especially, as we shall see, in life history priorities and the importance attached to individual well-being (Barnard & Hurst 1996). Indeed, the very concept of 'welfare' could be regarded as an anthropomorphic conceit imposed on other species by one with a long life span and long period of parental care in which attaching a high priority to future survival (and thus maintaining well-being) yields reproductive dividends. The conceit is exacerbated by the fact that the comfort and health criteria flowing from it arguably do not even serve our own species well in terms of individual welfare (see Barnard & Hurst 1996). That species, and individuals within species, are likely to differ in the priority attached to future survival is an axiom of life history strategy theory, and should ring alarm bells in the context of the above. So how can we accommodate such fundamental differences within a concept of welfare?

Adaptive Cost Gauging, Decision-making Rules of Thumb and Suffering

The problem with suffering is that it is a private subjective state inaccessible to an external observer. Allowances for it therefore have to be made on some kind of 'benefit of the doubt' basis, but on what should this 'benefit of the doubt' be based if not the anthropomorphic criteria referred to above or other comparisons with humans, such as those involving apparent cognitive processes (e.g. Mendl & Paul 2004; Paul et al. 2005)? Barnard & Hurst (1996) have argued that it should be founded on a thorough understanding of the animal's decision-making rules of thumb in the context of its adaptive life history strategy and thus trade-off between survival and reproduction. Their point is that positive and negative subjective states can be viewed as proximate mechanisms gauging the canonical (reproductive) cost of the animal's current state. Thus pleasant sensations, such as a nice taste or orgasm, gauge the likelihood that the animal's actions (eating a food item or copulating) will reap reproductive benefits, while negative ones, such as increasing pain or fatigue, gauge the likelihood that they will inflict reproductive costs (e.g. from overzealously defending a territory). Barnard & Hurst (1996) argued that such adaptive cost gauging, where it involves negative subjective states, should not merit the label 'suffering' because the animal is simply trading off activity costs against their reproductive benefit. As long as it is free to make the trade-off on its own adaptive terms (so as to maximize lifetime reproductive success), the animal is not under any imposition or in a situation into which it has not willingly entered. Thus, any 'clinical' sequelae, such as raised 'stress' hormone levels, reduced immunocompetence or weight loss, will

not be indicators of likely suffering but of what Barnard & Hurst (1996) refer to as adaptive self-expenditure.

This leads to a very different view of welfare from the traditional one in which homeostatic coping mechanisms are designed to maintain the well-being of the individual, and suffering is invoked when the animal fails to cope (Broom 1986; Broom & Johnson 1993). In the adaptive self-expenditure view, welfare is equated, not with individual well-being (the fallacy of individual preservationism, as Barnard & Hurst (1996) put it), but with the animal's ability to 'spend' itself in the manner dictated by its adaptive life history strategy. If 'suffering' is possible at all, and whatever the form it may take in different species, it is reserved as a subjective 'state of emergency' experienced by the animal when it is forced to act outside the adaptive bounds of its life history strategy. Since any such 'suffering' remains privately invisible, however, the most reasonable basis for recognizing when it is likely (and thus giving the benefit of the doubt) is by understanding when the animal is constrained to behave beyond the competence of its decision-making rules of thumb, since these have evolved to serve its adaptive needs within the framework of its life history strategy and environment of evolutionary adaptation (EEA) (Bowlby 1969; Mace 1995; Barnard & Hurst 1996). Such violations might arise, for example, when the animal is put into a novel or impoverished environment that is a poor analogue of its natural one, and might include the squashing of normally resilient behaviours within the animal's time budget, normally adaptive responses to a situation having an inappropriate outcome, decision-making paralysis ('limbo') caused by a lack of opportunity to perform a next-in-priority behaviour, and other infringements of the animal's ability to behave adaptively (McFarland 1989; Barnard & Hurst 1996). Of particular importance here are violations of the animal's perceptual rules of thumb (how it perceives and models the world around it for its own adaptive ends), which may lead to vastly different perceptions of objects and events from our own (e.g. Ewert 1980; Milligan et al. 1993; Dawkins 1998; Barnard 2004; Evans et al. 2006), and conditionality rules governing the modulating influence of developmental experience on potential subjective states and decision making (e.g. Burman & Mendl 2003; Paul et al. 2005). It is where such rules are infringed, then, that we might reasonably look for clinical corroboration of 'suffering' and be in a position to distinguish it from similar changes that simply reflect adaptive cost gauging. Rooting welfare concerns in the context of the animal's adaptive function like this is the basis of what I refer to as evolutionarily salient welfare. Two brief examples, both involving laboratory rodents, illustrate the point.

Immunity trade-offs in laboratory mice

The first concerns the regulation of testosterone secretion in relation to immunocompetence in male laboratory mice, *Mus musculus*, and highlights the importance of individual differences in adaptive self-expenditure.

Males put together in novel groups usually polarize into two easily identifiable social classes on the basis of aggressive and submissive behaviour (e.g. Mackintosh

1981; Gosling et al. 2000): dominant males that initiate significantly and disproportionately more aggressive behaviour than their companions, and subordinates that show much less aggression and more submissive behaviour and do not differ significantly in this regard among themselves (e.g. Barnard et al. 1996a). By analogy with their commensal wild counterparts (e.g. Hurst 1990, 1993; Barnard et al. 1991), dominants and subordinates can be seen as representing different life history strategies centred on competitive ability (Barnard & Behnke 2001, 2006). Competitive dominant males can command access to limited resources, such as food and nesting sites, and invest heavily in the reproductive opportunities this brings. Less competitive males cannot compete for resources so have to make do with sneaking opportunistic matings as and when they can.

A prediction that follows from this is that dominant males will be more likely to trade-off future survival for short-term reproductive gain than subordinates, which would do better to safeguard future survival and maximize the likelihood of chance matings. One way of regulating the trade-off might be to link the secretion of the potentially immunodepressive sex hormone testosterone (e.g. Grossman 1985; Folstad & Karter 1992) to current immunocompetence. Barnard et al. (1996a) found that subordinate males did exactly this by regulating the secretion of testosterone over the period of grouping in relation to their current circulating antibody (total IgG) titre. As a result, their resistance to a subsequent infection of the blood protozoan *Babesia microti* was unaffected by testosterone. Dominants, in contrast, did *not* regulate their secretion of testosterone in relation to antibody levels, with the result that testosterone reduced their subsequent resistance to infection. Thus, within social groups, individual males responded in apparently different adaptive ways to the reproductive implications of their social environment. Further evidence that this might reflect an adaptive reproductive trade-off comes from a later study of experimentally immunodepressed males (Barnard et al. 1997a, b). Males of both rank categories that had had their cellular immunity temporarily depressed by antithymocyte serum downregulated both testosterone and behaviours such as aggression that were generally associated with reduced immunocompetence, but performed more of those behaviours, such as sleep, that were associated with enhanced immune function (Barnard et al. 1997a). The really telling point, however, was that the regulation of both testosterone and behaviours affecting immunity in immunodepressed males was abolished when female odours were present in the environment (Barnard et al. 1997b).

Taken together, therefore, these results suggest that males bring costly physiological mechanisms into action only if it is reproductively worthwhile to do so. Thus, dominants are more prepared than subordinates to risk their future survival by secreting testosterone indiscriminately because they are in a better position to secure matings in the short term. However, both classes of male are prepared to risk it if current reproductive opportunity seems high enough (there is a lot of female odour about). These are important distinctions if one is to attempt to

impose welfare requirements on these animals, because they demand different criteria if they are to recognize the respective self-expenditure choices of different individuals.

The studies above also offer a cautionary tale with respect to welfare initiatives. Environmental 'enrichment' is an increasing enthusiasm in the world of welfare regulation (e.g. Markowitz 1982; Chamove 1989; Patterson-Kane 2004; Buchanan-Smith et al. 2005) and stems from the laudable aim of providing heterogeneity and naturalistic diversity in otherwise monotonous captive environments. 'Enrichment', however, is a loaded subjective term, designed to equate increased complexity with enhanced living conditions. While this equation appears to be supported by at least some lines of evidence (Würbel 2001), just like the concept of 'welfare' itself, 'enrichment' requires contextualizing in relation to the animal's adaptive rules of thumb and EEA and cannot simply be assumed to equate to increased complexity. A case in point comes from some of the subtle conflicts it can generate. Barnard et al. (1996b), for example, studied the effects of adding nestboxes and shelving (\equiv 'enrichment') to the cages of groups of male mice on the testosterone/immunity trade-off discussed above. They found that mice in enriched cages were significantly more aggressive, something that has been found by other authors (e.g. McGregor & Ayling 1990; Haemisch & Gartner 1994), and less resistant to a later infection of *B. microti* than mice from nonenriched cages. Barnard et al. (1996b) also found negative partial regression relationships between aggression received and both circulating antibody titre (total IgG) and resistance to *B. microti*. Thus, the enriched cages appeared to provide a more hostile environment, probably because the discrete physical features of the furnished cages provided a focus for aggressive defence by dominant males, an adaptive feature of their reproductive behaviour (Hurst 1987a, b). Did mice 'care about' this in the sense of attempting to offset the apparently deleterious effects? Evidence from the regulation of testosterone secretion suggests they did. In the enriched cages, and in contrast to Barnard et al.'s (1996a) results earlier, *both* dominant and subordinate males modulated testosterone secretion in relation to total IgG. As a result, neither category of male showed a testosterone-dependent reduction in resistance to *B. microti*. In the less hostile nonenriched cages, testosterone was decoupled from total IgG and mice *did* suffer a testosterone-dependent reduction in resistance (Barnard et al. 1996b). So, in the enriched cages, mice appeared to take precautionary measures to safeguard immunocompetence in the face of apparently environmentally induced immune depression, whereas they were prepared to tolerate an impact of testosterone in the more benign nonenriched cages. Interestingly, time spent in the nestboxes and on the shelves correlated positively with total IgG concentration and resistance, so 'enrichment' did appear to offer benefits in terms of well-being, but only in the context of an overall drop for the environment as a whole. Once again, therefore, effects of conditions imposed on animals need to be evaluated in the context of different individual strategies of self-expenditure.

Social housing in laboratory rats

The second example comes from a study of housing conditions in laboratory rats, *Rattus norvegicus* (Hurst et al. 1997, 1998). Although rats are social animals, they are often housed singly in laboratories to prevent problems with aggression and other sources of social stress or standardize social experience for experimental purposes (e.g. Brain & Benton 1983; Mormede et al. 1990). That this 'works' in terms of classical clinical yardsticks of stress is suggested by the fact that singly housed rats have reduced circulating levels of corticosterone and less early stage organ pathology than socially housed counterparts (Hurst et al. 1997). But which kind of environment would rats choose if given the option? By housing singletons and groups either side of partitions allowing different degrees of detectability across them (ranging from solid metal sheets to open mesh), Hurst et al. (1997, 1998) were able to show that singletons spent significantly more time at the partition, attempting to interact with grouped animals on the other side, than vice versa, and that time at the partition increased with the opportunity for interaction across it. Similar preferences for groups have been obtained in other choice experiments with rats (e.g. Patterson-Kane et al. 2002, 2004). Thus rats appeared to seek a social environment in which clinical indicators suggest their welfare, in the traditional sense of individual well-being, will be compromised, but an environment, of course, in which their life history priorities have evolved and their reproductive opportunities lie (Barnett 1975; Lore & Flannelly 1977). The rats' apparent choice thus makes functional sense in terms of adaptive self-expenditure.

PAROCHIALIZING THE REGULATION DEBATE: IMPLICATIONS FOR SCIENCE AND WELFARE

While evolutionarily salient welfare should inform animal welfare policy in any circumstances, it self-evidently does not, and one reason for that, I suggest, is because welfare policy and regulation within animal science is being driven largely by the laboratory utilitarian interests referred to earlier. It is not difficult to see why this should be. Medical benefits for humans are seen by many scientists as the strongest selling point for animal experimentation in the public domain; a tack that is also, not surprisingly, taken by the powerful pharmaceutical industry. This cuts a lot of ice with legislators and politicians and is the reason for the explicitly biomedical line taken by the European Coalition for Biomedical Research (<http://www.ecbr.eu>) recently established to coordinate European scientific interest responses to the draft revision of EU Directive 86/609 on animal experimentation, a Directive that affects Europe-wide legislation on scientific work with animals. While the Directive applies to all animal science, lobbyists see medical benefits from animal work as the key to getting the ear of European politicians, and thus couch their responses to the draft in terms of the laboratory science that underpins it. Of the 34 professional societies and associations so far making up the Coalition 28 are wholly or partly concerned with biomedical research, so mainstream organismal biology is vastly

underrepresented in the process. Tellingly, the recent survey of animal scientists and special issue articles on animal experimentation by *Nature* on 14 December 2006 (Vol. 444, No. 7121) also reflects almost exclusively the interests and procedures of laboratory biomedical science.

This bias is becoming institutionalized. For example, in its mission statement, the recently established U.K. National Centre for the Three Rs (NC3Rs) (<http://www.nc3rs.org.uk>) declares that 'The NC3Rs is dedicated to the 3Rs - replacing, refining and reducing the use of animals in research and testing licensed under the Animals (Scientific Procedures) Act 1986', that 'Optimal laboratory animal welfare is critical for scientific, legal and ethical reasons', and that its aims will be achieved by 'Supporting the UK scientific community's commitment to best practice in all aspects of laboratory animal science and welfare'. It also states that 'Replacement is the ultimate aim for the Centre'. The inception of the NC3Rs and its general *raison d'être* are, of course, to be welcomed. One can also understand the inherent bias towards laboratory animal science given the organization's roots in the U.K.'s Medical Research Council. However, the overtly limited scope of its mission leads to some serious concerns in terms of applying the three Rs across animal science as a whole, only one aspect of which is appropriate to the conditions and aspirations of the NC3Rs statement. Confusion arises immediately, for example, because U.K. Home Office licensing extends beyond the boundaries of laboratory/utilitarian research, and because ethical concerns, to which the three Rs apply, extend beyond procedures coming under Home Office scrutiny (see, for example, the ASAB/ABS ethical guidelines referred to earlier). Thus casting its mission in terms of laboratory procedures falling within the purview of Home Office licensing is doubly limiting.

There is also an issue with Replacement as the organization's ultimate aim. This is partly because Replacement cannot be a logical objective where animals themselves are the object of study (as opposed to exploitable resources; see also Griffin & Gauthier 2004), which is the case for most mainstream animal biologists (the argument that Replacement refers to procedures rather than animals [Russell & Burch 1959] makes no difference here, since the aim in either case is to remove the need to experiment on animals), but also because Replacement requires a degree of confidence in the current state of knowledge about a system that may not be warranted. The animal biology literature is replete with examples of models and conclusions, long held to be the last word on a particular problem, being overturned and radically revised some years later when new ideas or discoveries have prompted review (the classic textbook model of the neural control of the escape swimming response in the sea slug *Tritonia* [see e.g. Willows & Hoyle 1969; Katz & Frost 1995] is a good example). An overenthusiastic pursuit of Replacement in response to fickle, short-term pressures of public and political opinion thus carries a serious risk of premature bridge burning. While this may not be much of an issue if, say, cells or tissue are being cultured simply to harvest an enzyme or hormone, it is very likely to be one if what is at stake is the holistic functioning of a system in relation to, say, drug efficacy. This leads to a more general

consideration of what the three Rs should mean when it comes to animal science as a whole.

What Should the Three Rs Mean?

Although Russell & Burch's (1959) three Rs are the chief guiding principle in welfare regulation, there is a considerable lack of clarity and consensus over what they should mean in practice, even within relatively standardized laboratory environments (Buchanan-Smith et al. 2005; Schuppli & Fraser 2005; Vorstenbosch 2005). The reasons for this are several, and often stem from different opinions or assumptions as to what effects and actions fall within the definition of a particular R (Schuppli et al. 2004; Buchanan-Smith et al. 2005), or even as to how the particular R should be defined in the first place (Buchanan-Smith et al. 2005). The three Rs can also conflict with one another in terms of ethical objectives, leading to dilemmas in regulatory decision making (de Boo et al. 2005). From the point of view of animal science as a whole, however, it is what the three Rs should mean in the broad tranches of animal biology that lie beyond the clinical/commercial laboratory setting that gives most cause for thought.

As Griffin & Gauthier (2004) have pointed out in their excellent consideration of the three Rs in wildlife research, criteria for the respective Rs in curiosity-driven animal biology may differ fundamentally from those in a highly controlled laboratory environment. Replacement per se is usually not an option (see above), and criteria for Reduction and Refinement may depart substantially from the classical experimental design and statistical protocols of laboratory work (Festing 2003, 2004a; Griffin & Gauthier 2004; see also Schuppli & Fraser 2005). This may be especially so in the case of field studies, where what Albrecht (1999) has referred to as an ecocentric focus (concentrating on the ecological integrity of the system) often replaces the individualist one of traditional welfare considerations (Griffin & Gauthier 2004). Albrecht's distinction has resonance with that between adaptive self-expenditure and individual well-being, in that the adaptive self-expenditure view also argues for departure from traditional yardsticks for the legislative quartet of 'pain, suffering, distress and lasting harm' on the basis that these may not reflect impositions on the animal as much as adaptive choice (see above). This has important implications for what one might want to regard as Refinement in a welfare context, where arguably the emphasis should be on tailoring environments and procedures to harmonize with the animal's adaptive rules of thumb rather than on maintaining individual well-being. Of particular importance is that Refinement should embrace individual differences in adaptive rules of thumb and recognize diversity in chosen strategies of self-expenditure within any given context (e.g. Clutton-Brock et al. 1982; J.L. Hurst et al. 1996, 1999; Barnard & Behnke 2001; see above), something that is also likely to have consequences for decisions about sample size and approaches to Reduction. Arguably, therefore, the most urgent requirement under Refinement is for fundamental research on species- and individual-specific behaviour.

The Biomedical/Laboratory Science Trap

Arguments based on welfare as adaptive self-expenditure rather than well-being highlight the hazards inherent in the current over-focus on laboratory utilitarian science. Internalizing the loop between the development of regulatory policy and the practices it is intended to regulate within the highly controlled environments of laboratory utilitarian research risks unintended, counterproductive consequences when policy and perceived 'good practice' are extended, as they already are, into the much less controlled (and often less controllable) environments of open-ended curiosity-driven studies.

Much 'good practice' in laboratory settings is characterized by a desire for standardization (e.g. in stocking densities, laboratory strains, environmental 'enrichment', temperature and humidity, air exchange rate; e.g. Festing 2001, 2004b; Marashi et al. 2004; Patterson-Kane 2004; Brandstetter et al. 2005). Not only is this inimical to the environmental requirements of much evolutionary and ecological curiosity-driven research, where natural variation in physical, social and genetic environments is an essential backdrop to the biology under consideration, but it also constrains the external validity, and thus general explanatory power, of the very laboratory protocols that embrace it (Würbel 2000, 2002; Cuthill 2007). Furthermore, the criteria for standardization are largely based on either the anthropomorphic welfare considerations discussed earlier, or on practical (husbandry or experimental) or analytical (statistical) convenience, often with uncritical generalization across contexts (e.g. environmental 'enrichment'). Thus standardization is likely to conflict with the principles of evolutionarily salient welfare, and itself be a source of welfare concern.

In short, therefore, the domination of biomedical/commercial interests and a laboratory animal mindset risks regulation that is inappropriate to large swathes of animal science, and encourages concepts of welfare that are at odds with a properly animal-centred approach. So what can be done about it?

WHERE NOW?

Organismal animal biology, in the sense that evolutionary biologists, ecologists and zoologists recognize it, is at the moment a tiny voice in the debate about the regulation of animal science. If it does not become louder, and participate much more actively in the media, political consultations and national and international forums that drive these issues, it will find itself pushed into an ever tighter corner in terms of its freedom to operate. This will be bad news for animal science and bad news for animal welfare. Animal behaviour has a prime role to play here since it is the branch of animal science that is concerned with the functional design of animals and thus provides the evolutionary lens through which underlying anatomy, physiology, biochemistry and genetics should be viewed. Indeed, one might almost paraphrase Dobzhansky (1973) and say that: 'Nothing in biology makes sense except in the light of the functioning whole organism'. Even notable exceptions to

the maxim, such as selfish genetic elements (Hatcher 2000), extended phenotypic effects (Dawkins 1999) and the genetic conflicts inherent in genome evolution (L.D. Hurst et al. 1996; Burt & Trivers 2006) emerge by comparison with the adaptive interests and mechanisms of individual organisms. But animal behaviour has much more to say than this. In its concern with the decision-making propensities of animals, it provides the only avenue we have for establishing a meaningfully animal-centred concept of welfare, and for contextualizing clinical, physiological and other changes that on their own can provide only equivocal evidence from a welfare point of view. The science of evolutionarily salient welfare is barely in its infancy; a vigorously expanding programme of behavioural studies is essential if we are ever to have a sound framework for animal welfare policy. This means much more experimental animal biology and an approach to regulation that is properly inclusive of the branches of animal science and founded on robust evolutionary understanding. We who study behaviour have a particular responsibility in this regard and should make sure our voices are heard both in the ongoing public and political debate about animal experimentation, and in the organizations, conferences and journals concerning themselves with animal welfare. If we do not, and we wind up saddled with inappropriate legislation based on skewed notions of welfare and good practice, we shall have only ourselves to blame.

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