

ON COMPARING THE BEHAVIOUR OF ZOO HOUSED ANIMALS WITH WILD CONSPECIFICS AS A WELFARE INDICATOR

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Abstract

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It is commonly assumed that animals suffer if they cannot perform behaviours seen in wild conspecifics. Although comparisons with the behaviour of wild conspecifics are a popular method of assessing the welfare of captive animals, their validity has not been fully assessed. Homeostatic models of motivation suggest that many behaviours are stimulus driven rather than internally generated. Thus, it is possible that the non-performance of some wild-type behaviours does not necessarily compromise animal welfare, unless welfare is defined as being compromised by such non-performance. The flexibility of wild animal behaviour and the fact that animals free to perform the complete range of wild behaviours can suffer, must also put into the question the validity of such comparisons. Technical criticisms also arise when one considers the difficulty of constructing accurate and unbiased time budgets for wild animals. It is possible that the expressions of wild-type behaviours correlate with enhanced welfare, rather than cause enhanced welfare. Thus, if the consequences of behaviour are more important than the expression of behaviour itself, environmental enrichment does not necessarily need to rely upon the performance of wild-type behaviours for the improvement of animal welfare. Therefore, although behavioural comparisons with wild animals can be considered as potentially useful indicators of behavioural differences, they cannot always be relied upon to give an objective assessment of animal welfare. To make an assessment of welfare, behavioural comparisons with wild animals should be used in conjunction with other techniques to demonstrate that the consequences of non-performance of wild behaviours results in impoverished welfare.

Keywords: *animal welfare, behaviour, behavioural needs, captive, motivation, wild*

Introduction

The behaviour of a wild animal, which we define as: 'the behaviour expressed by an animal subject to environmental and evolutionary pressures with minimal human intervention', is often used as a bench mark by which the welfare of captive animals can be assessed (Thorpe 1967; Heidiger 1969; Lindburg 1988; Fraser & Broom 1990; Chamove & Anderson 1989; Chamove 1989; Shepherdson 1989a; Bayne *et al* 1992). Thorpe (1965) and Martin (1979) argue that animals have to perform the full repertoire of behaviours shown by free-living conspecifics, for suffering to be avoided. Thorpe (1967) further argued that animals suffer

more if they are unable to express those behaviours that occur most frequently in the wild. The logic behind such comparisons with wild animals seems to lie in the assumption that a healthy wild animal is likely to have adequate welfare. Thus, if a captive animal behaves in a similar way, it is plausible that its welfare is comparable. Assumptions such as these, though not based on a scientific foundation (Hughes & Duncan 1988), have remained relatively unquestioned (Markowitz 1982). They have, however, led to the condemnation on welfare grounds, of environments in which animals are unable to express the full natural behavioural repertoire.

However, it can be argued that the performance of all behaviours is not essential for adequate welfare, as animals behaving in a way different from wild conspecifics are not necessarily suffering.

Definitions and measurements of animal welfare with reference to the zoo environment

In considering whether the expression of wild-type behaviour is essential for the welfare of zoo animals, one must consider how animal welfare is defined. If Bayne *et al*'s definition of behavioural well-being (1992), that is: 'the manifestation of a behavioural repertoire which approximates that seen in the species under free ranging conditions', were synonymous with welfare, then the expression of wild behavioural patterns is essential. However, 'welfare' is a term with a bewildering array of definitions, each placing emphasis upon different aspects of an animal's existence (see Mason & Mendl 1993).

Fraser and Broom (1990) and Barnett and Hemsworth (1990) emphasize the relationship between welfare and genetic fitness, that is the measure of the rate of increase of a genotype relative to other genotypes in a population (Futuyama 1986). Archer (1979) illustrates how stress and poor welfare can reduce the fitness of an animal by lowering longevity and reproductive output. However, the emphasis upon physiological and physical measures of animal welfare has been criticized by Stolba and Wood-Gush (1984) and Thorpe (1967), primarily as it is common for agricultural animals with apparent low welfare status to have high fitness, in that they breed and grow well. There are, for example, coping mechanisms, or consequences of coping that may not reduce fitness and yet still indicate reduced welfare. Cronin (1985) for example has shown that temporarily at least, the more stereotypic a sow is, the larger second and third litters it is likely to have. Translated literally, the emphasis upon fitness could also infer that a sterile animal has a lower welfare status than a fertile one.

Stolba and Wood-Gush (1984), however, consider motivational balance to be critical for adequate welfare. Such a balance they say, will require the fulfilment of behavioural needs, an idea that arose largely under the influence of Lorenz's psychohydraulic model of motivation (Lorenz 1950; Hughes & Duncan 1988). Here it was proposed that motivation would build-up independently of external stimuli and could only be reduced by the performance of motivationally driven behaviour. Thus, if an animal is prevented from performing such motivated behaviours, behavioural indicators of frustration may become manifest (Ewbank 1985), and reduced welfare could result (Hughes & Duncan 1988). However, since the appearance of Lorenz's model, a variety of 'homeostatic' models have been suggested (Hughes & Duncan 1988). It is now realized that many behaviours are in fact stimulus driven rather than internally generated, as motivation to express certain behaviours will not increase without the presence of the appropriate internal or external stimulus (Stolba

& Wood-Gush 1984; Ewbank 1985). Thus, it may be considered that the expression of a particular behaviour is not necessary for adequate welfare (Baxter 1983), providing that all the animal's environmental requirements are met and therefore motivation to express the behaviour is not triggered. In some cases, however, the expression of a behaviour may be important irrespective of any physiological imbalance. For example, the tongue-playing behaviour of giraffes seems to be connected with the 'need' to express normal appetitive feeding behaviour (see Sato & Takagaki 1991), rather than with a physiological need to feed. Thus, the performance of a consummatory act is not necessarily made obsolete by satisfying physiological parameters alone (Stolba & Wood-Gush 1984). Thus, some behaviours may have to be expressed for adequate welfare, irrespective of physiological needs (Jensen & Toates 1993). Such behaviours could be described as 'ethological needs' (see Jensen & Toates 1993).

Other welfare scientists place more emphasis upon the psychological aspects of animal welfare, which are likely to reflect motivational and physiological states. Dawkins (1990) for example, considers welfare to be compromised in an animal experiencing an unpleasant mental state. Psychological aspects, however, are difficult to measure. So, although welfare is not defined with physiological parameters, such parameters are commonly used as a means of identifying the possibility of such unpleasant psychological states (see Barnett & Hemsworth 1990; Manser 1992). There are, however, technical problems with physiological measures, and problems of interpretation (Mason & Mendl 1993). More relevant to this discussion is the unsuitability of these measures in the zoo environment (Shepherdson 1989a), as they are commonly invasive, which can be difficult, dangerous and publicly unacceptable.

Behavioural measures, however, have a number of advantages. They are non-invasive, give an instantaneous welfare measure, require little in the way of specialized equipment and are possibly more sensitive in that they identify the first type of coping response that an animal is likely to make (Duncan & Mench 1993). Thus, as a result of the inadequacy of fitness as a welfare measure, the difficulties of assessing mental and motivational states, the problems in collecting and interpreting physiological measures, and the relative ease of collecting behavioural data, an overemphasis may have been placed comparing behaviour in wild and captive animals as a zoo welfare measure.

The assumption that the expression of wild-type behaviour is indicative of high welfare status

The extent to which the behavioural differences between captive and wild animals can be used as a welfare indicator is a matter of contention. It can be argued that although the expression of wild-type behaviour may well correlate with adequate welfare, it may not be the expression *per se* that results in welfare benefits, rather the consequences of that expression. For example, it is believed that the health status of captive animals increases with the greater variety of stimuli and food types they are exposed to, together with the variety of muscles they use (Chamove & Moodie 1990). Lindburg (1988) emphasizes the link between more natural feeding behaviour and oral health in both Amur tigers (*Panthera tigris altaica*) and cheetah (*Acinonyx jubatus*), where animals fed carcasses suffered less gingival health problems, plaque formation and focal palatine erosion than animals fed formulated diets.

There is less evidence, however, that performance of wild-type behaviour *per se* in zoo animals is important. It is possible that, for many behaviours, the animals suffer more from the consequences of non-performance than from the non-performance itself. It may be argued that this is unimportant as wild-type behaviour results in enhanced welfare and the mechanisms for this are irrelevant. We would argue, however, that if behavioural expression is not important, but the consequences are, then alternative behaviours could be elicited by management techniques and environmental enrichment that still enhance welfare without the need to provide for difficult wild-type behaviours. If, for example, control (being able to choose which behaviour to express) is more important than the expression of wild behaviours (see Weiss 1972; Markowitz 1982), it may only be necessary for the animal to express control over its behaviour and its environment without having to rely upon wild-type behaviours. Studies on captive primates have shown that wild-type behaviours are not essential for welfare to be improved (Markowitz *et al* 1978; Chamove 1989).

Many animals now live wild in environments other than those in which the species originally evolved, and as a result, perform previously unseen behaviours. The exploitation of rubbish tips by numerous species could be cited as an example. There are comparable behavioural changes that occur in captivity that are also unlikely to indicate reduced welfare status, but are considered to indicate such, simply because they occur in the captive context. For example, a captive giraffe given a grassy paddock may graze more than a wild counterpart, and may also spend a greater proportion of the daylight hours lying down. Both these behaviours are rarer in the wild, presumably out of necessity rather than out of choice, grazing being rare due to lack of suitable grazing throughout most of the year (Dalton 1987), and lying being rarer in wild adults because of the risks of predation. Should the inclusion of these behaviours in the captive ethogram then be considered as a welfare problem? We would suggest not, unless these behaviours have consequences that result in lowered welfare, such as scouring due to excessive grass intake.

Changes from the wild ethogram should therefore be associated with negative effects or conditions for them to be implicated in reduced welfare. For example, stereotypic behaviours arise in sub-optimal conditions and circumstances, and may also result in physical damage (Mason 1991). As a consequence, stereotypies could be considered as valid welfare indicators. Other qualitative and quantitative behavioural changes should also be treated in a similar way. Beaver (1980), and Leyhausen (1979) indicate that predatory behaviour is a 'need' in cats, since they perform hunting behaviour even when their nutritional requirements for food have been met. However, observations in the wild have shown that given the opportunity, big cats will readily scavenge for all of their food (Lindburg 1988; Jackson 1992). Thus, animals will override the 'need' to hunt in the wild. However, the inability to hunt in captivity is considered a welfare problem, without any demonstration that this causes suffering. Why should this be? Are we allowing our scientific judgement to be clouded by our intuitive perception? We suggest that it is essential either to prove that the animal is motivated to perform a particular behaviour and is chronically prevented from doing so, or that it suffers in some way by not being able to perform a behaviour.

That the wild environment leads to optimal welfare itself is open to debate. The welfare of a substantial proportion of wild animals free to express their full behavioural repertoire is compromised by hunger, injury, disease, parasitism, temperature extremes, etc. For example, 86 per cent of a population of wild wood mice were found to be infected with a

single nematode species, with worm burdens as high as 207 per animal (Gregory *et al* 1992). As this was sufficient to depress individual survival, it is certain that it will have a negative effect upon welfare. Predation will inevitably compromise the welfare of the prey individual, and yet it is a common fate for many, if not most, wild animals. As many as 73 per cent of giraffe calves are predated on in their first year (Skinner & Smithers 1990), and 20 per cent of all giraffe are taken annually by lion alone (Owen-Smith 1988). Animals also cause considerable suffering to conspecifics in the wild, something that effective zoo management can also eliminate. For example, 5 to 10 per cent of musk ox are killed annually from rutting injuries, and 23 per cent of red deer stags are injured annually due to rutting behaviour (Clutton-Brock *et al* 1979). Many people rightly accept these as natural, and so would not consider them a welfare issue, despite their severe welfare implications. However, there are other factors that humans have introduced into the wild, such as hunting, trapping, pollution, etc, all of which combine to compromise the welfare of wild animals, and as such, are a welfare issue. It has also been suggested that the wild environment may be more mundane than many people would at first consider (Shepherdson 1989a; Dalton 1987; Moss 1989), and that wild animals are likely to experience behavioural frustration. For example, being unable to feed or mate in the presence of a dominant animal (although this is rarely as chronic a problem in the wild as it is in the zoo). Thus, it may be that life in the wild is not as ideal for welfare as might first be considered. Markowitz (1982) claims that it may in fact be possible to improve upon nature by minimizing health problems, and yet still provide for an animal's behavioural needs.

It is not disputed that the expression of some behaviours are essential for adequate welfare of a zoo animal. However, the statements made by Thorpe (1967) and Martin (1979) imply that the full behavioural repertoire of an animal is essential for adequate welfare. This view is endorsed by the UK's Farm Animal Welfare Council (FAWC) (Dawkins 1990), but this may be flawed and lead to contradictions. For example, FAWC claim that freedom from fear and freedom to express normal behaviours are essential for adequate welfare (Anonymous 1992). The performance of anti-predator behaviour, mediated by fear therefore, has ambiguous welfare implications. Chamove and Moodie (1990) state that such alarming events can result in enhanced welfare as they cause a wider range of normal behaviour. This may be the case, but the actual performance of predator avoidance behaviour will not enhance welfare directly, though its consequences may.

Other behaviours that are essential for survival in the wild are 'encouraged' by natural selection by being rewarding to the animal. Denying an animal the opportunity to perform a rewarding behaviour is denying it potential reinforcement, and its welfare may therefore be reduced in relation to an animal free to perform that behaviour. Whether an animal can suffer by not performing a behaviour it has never performed is open to debate (see Wemelsfelder 1989). However, the non-performance of a behaviour may leave a void that itself may result in boredom, redirected behaviour, vacuum activities, stereotypies or reduced health. Thus, the absence of a behaviour should be considered for its consequences. For example, the suffering caused by the non-performance of a specific behaviour cannot yet be adequately measured. However, the effects upon an animal's health resulting from the inactivity due to the non-performance of a specific behaviour can be measured, as can the replacement behaviours. Such an approach may allow the welfare implications of the non-performance of particular behaviours to be assessed.

The assumption that the animals suffer more if unable to express behaviours that are of a long duration is also likely to be flawed. Behaviours that are important to the animal are not necessarily those that are of the longest duration (Dawkins 1983). If motivation was equivalent to duration then one might assume that zoos were providing well for the requirements of their captive carnivores, noted for their inactivity both in captivity and the wild. Snyder (1977) describes this inactivity as a problem in zoos, but does not state why. It is known that many predatory animals spend a large proportion of their time resting in the wild (Herbers 1981). Lions for example, are known to spend up to 75 per cent of their time resting (Schaller 1972), similar to that seen in captive carnivores (Veasey 1993). It can therefore be seen that zoos may have suffered undue criticism as a result of wild comparisons, as they are chastised for not fulfilling the behavioural requirements of their animals, and yet they are also condemned for allowing their animals to express a normal level of inactivity.

The question then arises of whether the expression of wild behavioural patterns in the wrong context, or possibly without the appropriate stimuli, is sufficient in satisfying the needs of that animal. For example, it is plausible that a racoon has a need to wash its food in that it inappropriately washes soluble food in captivity (Chamove & Anderson 1989). If food washing is a need, then does this behaviour satisfy it? According to Abegglen (1974) it probably does, as he states that the physiological and motivational requirements may be satisfied separately. So, an animal may perform hunting behaviour, for example using an automated device, and yet be fed from a bowl and still be satisfied. It is also important to elucidate whether performance *per se* is important when considering the relevance of stereotypic behaviours. Pacing for example, is abnormal in terms of context and frequency in relation to the wild behaviour of the same species. However, the motor patterns are similar to those shown by wild individuals; consequently the animal may increase muscle tone and thus general health status.

The belief that animals have a need to express the full range of their behavioural repertoire is reliant upon Lorenz's now somewhat discredited psychohydraulic model of motivation (Hughes & Duncan 1988). The use of behavioural comparisons with wild animals as a welfare measure must therefore be questioned. We do not doubt that some animals have a 'need' to express some behaviours (see Dawkins 1990), but we would argue against the implication that any missing behaviour indicates compromised welfare. The absence of a specific behaviour may result in reduced welfare, but ideally it should be demonstrated to do so, through consumer demand theory or behavioural resilience for example, rather than assumed to do so (Dawkins 1990). What is critical here is that there is not a need to perform all behaviours; predator-avoidance behaviour without eliciting stimuli being a classic example. A hen given the opportunity to dust-bathe will do so; but according to Ewbank (1985) behavioural indices of frustration are constant with or without the presence of litter. From this evidence one might conclude that the expression of dust-bathing behaviour is not a 'need'. Alternatively, the indices of frustration may be inadequate, and so attempts to assess how important dust-bathing is to the hen should be made (see Dawkins 1983). By analogy, a tiger will express predatory behaviour given the opportunity, but may not suffer from non-expression without an appropriate stimulus.

Logistical problems in comparing behaviour in wild and captive animals

Beyond the theoretical problems already outlined, there are considerable logistical problems in comparing behaviour in wild and captive animals:

- 1) There are difficulties in assessing the wild-type behaviour of an animal without influencing it (Isbell & Young 1993). Markowitz and LaForse (1987) stated that the captive servals in their study exhibited less activity than wild counterparts. However, in the wild, small cryptic animals are likely to be more visible when active than when resting, and are less likely to rest in the presence of humans. Subsequently, an over-estimation of wild activity levels may be made.
- 2) An animal's behaviour is highly dependent upon short and long-term, biotic and abiotic factors such as age, sex, season, weather, health status, predation pressure, etc. For example, Young (1993) has shown that foraging behaviour in pigs varies from 25 to 75 per cent of the time depending upon food abundance. In primates, estimates for foraging time vary from 25 to 90 per cent (Chamove 1989) and 7 to 65 per cent (Bayne *et al* 1992). Estimates for feeding time in giraffes vary from 53 to 72 per cent for females, and 43 to 55 per cent for males (Estes 1991; Owen-Smith 1988). Thus, comparing quantitative behavioural measures alone is of little use other than as a guide. The environment can also influence qualitative changes in behaviour of a species. For example, dunnoek mating behaviour is highly influenced by environmental factors (Davies 1992).
- 3) There is an increasingly large number of species that are rare or extinct in the wild. Zoo populations for many species may also be small, making studies difficult, and sample sizes small. Those animals that do survive in the wild often do so at the edge of their range (for example the Scottish Wild Cat), where behaviour will not be truly representative.
- 4) Due to the limited sample size in zoo populations, one may be forced to generalize across different subspecies or even species (Veasey 1993). The genetic composition of a zoo animal may therefore differ from its wild equivalent, thus compromising the validity of any conclusions made (Carter 1967). If one is only to compare wild and captive behaviour with direct genetic equivalents to avoid such problems, one is faced with difficulties such as the sub-species status of many animals being still in doubt, and many individuals, most notably giraffes exist in captivity as hybrids.
- 5) Changes will be apparent between the zoo and the wild, but the cut off point indicative of reduced welfare will require further research.
- 6) There is a possibility that zoo observations may be skewed as animals not fit enough to survive in the wild will survive in captivity.
- 7) Within both wild and captive populations there is considerable individual variation that makes interpretation problematic. In a study of 13 captive tigers, the proportion of time spent in stereotypic behaviour varied from 0 to 32 per cent of observed time, and between 0 to 8 per cent within a single enclosure (Veasey 1993).
- 8) Captive and wild behavioural measures are rarely carried out by the same observers (see Markowitz & LaForse 1987), and as a result, the validity of any conclusions that may be drawn must be questioned.

Discussion

According to Heidiger (1969): 'the standard by which a zoo animal is judged should be according to the life it leads in the wild.' In comparing wild and captive animal behaviour for use as a welfare indicator, results will inevitably indicate lower welfare for captive animals if any change in behaviour is assumed to indicate impoverished welfare. If one includes other measures such as biological fitness, disease susceptibility, annual mortality, longevity and parasitism, etc, comparisons may yield more balanced results. However, one is then faced with the problem of deciding whether, for example, the chronic frustration of a particular behaviour is better or worse than having an untreated physical injury.

In comparing behaviour of wild and captive animals, one assumes that the wild animal is content (Shepherdson 1989b). Though this may be true for most individuals of a species at any one time, in many cases it will not be, and it is likely that all wild animals will suffer at some point. In fact the wild is likely to compromise four of FAWC's five freedoms (Anonymous 1992), with only freedom to express normal behaviours being fulfilled. A good zoo, however, may only compromise an animal's freedom to express normal behaviours, and an excellent zoo may not even compromise this for some species.

In comparing wild and captive behaviour regarding animal welfare, one should ideally identify those behaviours that are most important to the animal. It may be possible to do this by assessing which behaviours constitute 'behavioural needs' (see Hughes & Duncan 1988) through the application of consumer demand theory (see, for example, Dawkins 1990). The extent to which these behaviours are suppressed should then be calculated from wild comparisons, and finally the consequences of that suppression estimated. This is undoubtedly a more time-consuming measure of animal welfare, but one that is likely to yield more credible results. By identifying which behaviours are important to the animal; it may then be possible for these behaviours to be satisfied specifically by environmental enrichment. Alternative methods have attempted the more difficult task of seeking ways of providing for all behaviours, rather than only those behaviours that have been shown to be important to the animal (see Stolba & Wood-Gush 1984).

Captivity undoubtedly alters behaviour, which is undesirable from an aesthetic and scientific point of view. However, we are less sure that it is inevitably undesirable from a welfare point of view, although we would not dispute that often it is. Animals will continually modify their behaviour to best fit their environment. Predation risk for example, has been shown to alter feeding behaviour (Milinski & Heller 1978; Suhonen 1993). Should this be considered as an indicator of reduced welfare as changes in captive feeding behaviour commonly are? A major problem with captivity is that all the essential requirements for survival are taken care of. Ungulates have little need to keep alert for predators and as such can compress their feeding time, carnivores are not forced to hunt and primates do not forage over long distances. Thus, though the missing behaviours may not be a need as such, they create a void that is itself a problem, as it must be filled and sometimes is by stereotypic behaviours. So it may be that the non-expression of a particular behaviour is not a problem, but rather the consequences are, that is the void that remains. Few would argue that humans suffer *per se* because our 'foraging time' is now compressed into weekly trips to the supermarket, the reason being that we have other things to do. Captive animals are rarely so lucky. It is our belief, that although it may be preferable to fill this void with natural behaviours, it is not essential. For example, the benefits of teaching great apes sign

language and of encouraging arboreal primates to forage on the floor using a wood chip substrate are accepted (Chamove 1989). However, behavioural engineers such as Markowitz have been criticized for allowing animals to express 'abnormal' behaviours (Hutchings *et al* 1978), which in terms of animal welfare may be unjustified. Markowitz, in his paper entitled 'In Defence of Unnatural Acts Between Consenting Animals' (Markowitz 1975), argued that just as humans use exercise bikes and rowing machines to negate the problems of limited exercise, captive animals should not be denied the opportunity to get stimulation and exercise in a comparable fashion. That animals appear to prefer to work for food, leads us to assume that animals enjoy doing things and exerting control over their environment (Markowitz 1982). Thus, it may be more important to provide animals with the ability to do this rather than merely providing animals with the opportunity to go through naturalistic motor patterns, that do not restore more natural contingencies.

There are also obvious problems of interpretation when assessing welfare by comparing wild and captive behaviour. Should wrist biting in captive macaques not be considered as a welfare problem because it occurs in the wild? (Grewal 1981). Conversely, should lying behaviour in giraffes be considered as a welfare problem just because it is rarer in the wild? (It may be that this indicates enhanced welfare in relation to the wild environment?) It is our belief that the consequences of any deviations from the wild behaviour of an animal should ideally be investigated before they are labelled as being indicators of poor welfare.

Although a captive animal performing all the behaviours within its wild repertoire is less likely to be suffering than one that is not, it does not follow that an animal not performing all of its wild behavioural repertoire is inevitably suffering. One cannot assume therefore, that the absence of wild behaviour indicates impoverished welfare without considering the consequences of this change. The link between similarity of wild behaviour and enhanced welfare may well exist, but it is not one that has been fully proved (Hughes & Duncan 1988). Even if such a link exists, it may be a mere correlation, as opposed to a causal link. For example, the welfare of an animal may be enhanced if it lives in an environment where it is able to express a near natural behavioural repertoire, rather than its welfare being enhanced directly by the expression of such behaviour (see Lindburg 1988). Measures other than a direct comparison with wild behaviour are ideally required in assessing the welfare of zoo animals, as this technique, though appealing, is not flawless. In the same way that welfare is affected by health, but not equivalent to it, behavioural expression affects the welfare status of an animal, but does not dictate it.

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