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Behavioural adaptation in the domestic horse: potential role of apparently abnormal responses including stereotypic behaviour

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Abstract

Classically, biologists have considered adaptation of behavioural characteristics in terms of long-term functional benefits to the individual, such as survival or reproductive fitness. In captive species, including the domestic horse, this level of explanation is limited, as for the most part, horses are housed in conditions that differ markedly from those in which they evolved. In addition, an individual horse's reproductive fitness is largely determined by man rather than its own behavioural strategies. Perhaps for reasons of this kind, explanations of behavioural adaptation to environmental challenges by domestic animals, including the capacity to learn new responses to these challenges, tend to concentrate on the proximate causes of behaviour. However, understanding the original function of these adaptive responses can help us explain why animals perform apparently novel or functionless activities in certain housing conditions and may help us to appreciate what the animal welfare implications might be. This paper reviews the behavioural adaptation of the domestic horse to captivity and discusses how apparently abnormal behaviour may not only provide a useful practical indicator of specific environmental deficiencies but may also serve the animal as an adaptive response to these deficiencies in an "abnormal" environment.

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1. Introduction

The horse's behavioural repertoire evolved in response to the challenges faced in its evolutionary niche of a herd-forming, grazing herbivore that usually avoids predation by flight. In the captive environment, many of these challenges have been removed. For

example, the stabled horse may be protected from predation provided with sufficient food and sheltered from climatic extremes but may not realise that these environmental challenges have been controlled. In other words, the psychological need to respond to environmental factors may still exist even when the biological need to perform adaptive behavioural responses has been removed. If these underlying mechanisms persist in captive horses, then it may lead to behavioural responses that are not seen in the natural environment and which are difficult to explain in terms

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of functional benefit. Examples include apathy and unresponsiveness, hyperresponsiveness and stereotypic behaviour. Welfare campaigners have suggested that such activities are an indicator of failure to cope with a poor environment because of their deviation from normal, functionally adaptive responses seen in free-ranging animals. An alternative viewpoint is that these activities may have a function for captive animals as part of their adaptation to the captive environment. For example, they could allow expression of highly motivated activities, thereby acting as a buffer against the physiological effects of distress or allow animals to gain some form of control over their immediate environment.

2. Assessment of adaptation to captivity

Before attempting to interpret apparently functionless behaviour, it is important to have a methodological framework to assess the relationship between behavioural responses and adaptation to man-made environments. Although the majority of work in this area has been conducted on farm animals, the principles apply just as well to horses as to any captive animal. Broadly speaking, there are three instances that can be adopted when considering the animals' ability to cope with captivity. These are the 'naturalness' of the behavioural repertoire, the biological functioning of the animal (its productivity and pathology) and its subjective state or feelings (Fraser et al., 1997). However, none of these three instances provides a satisfactory reference point for assessing an animal's ability to adapt to captivity when used in isolation. For example, allowing horses to express their full behavioural repertoire could mean exposing them to extremes of heat and cold, hunger or predatory stimuli, all of which may include negative experiences and may be completely avoided in a man-made environment (Hughes and Duncan, 1988).

Faced with these difficulties, Fraser et al. (1997) suggest an integrated approach to satisfy both animals and those who care for them. This approach assumes that welfare scientists should be concerned with the animal's psychological state, but that, as this cannot be measured directly, it must be inferred from measures that can be taken directly, including productivity, health, physiological measures and

behaviour. Within this framework, there should be concern both about the animal's species typical adaptive mechanisms and the challenges that it faces in the actual environment.

These challenges can take three forms. Firstly, they can be challenges that have been solved in the captive environment, but that the animal is still motivated to perform appropriate adaptive responses to. Stabled horses, for example, are generally provided with a nutritionally adequate balanced diet, but horses may still be motivated to express foraging and feed selection behaviour. This can be expressed as apparently undesirable behaviour in the stable. Secondly, there are environmental challenges which have not been fully controlled in the man-made environment so the animals must be allowed to express their natural adaptive coping responses. For example, in social housing, allowing horses to choose their social group and control their own personal space not only allows interactions with other horses but also provides opportunity for the horse to express control over its own environment. Thirdly, there are aspects in the man-made environment which involve challenges to which the horse may not be able to adapt, in which case, it is our responsibility to reduce the impact of these challenges or provide opportunities to adapt. For example, early weaning followed by social isolation may exceed the foal's capacity to adapt to environmental change, whereas later weaning into a mixed social group may reduce the impact of separation from the dam. This integrated approach should provide a scientific framework for pragmatic assessment of the impact of different husbandry practices on equine welfare, irrespective of the value of the horse under consideration or its place in our society.

3. Stereotypic behaviour as an example of adaptation to captivity

The application of this approach may be illustrated by the horse's behavioural responses to stabling. Apparently functionless, repetitive, stereotypic activities are commonly seen in stabled horses (McGreevy et al., 1995; Cooper and Mason, 1998; Nicol, 1999) and rarely if ever reported in free-ranging feral horses. Well-known examples include crib biting and wind sucking, box walking and weaving (Cooper and

Mason, 1998). More recently, several other activities have been described that fit the definition of stereotypy, including vertical head movement or nodding, as well as various oral activities, such as the licking or grasping of various stable fittings and even sham chewing or teeth grinding (Cooper and McGreevy, 2002). Horse owners commonly refer to these activities as stable vices, as if in some way, the horse is at fault. However, recent research indicates that these activities relate to the horse's attempts to adapt to the conditions in which they are kept and may fulfil all three categories of behaviour described by Fraser et al. (1997). They may represent firstly the expression of normal behavioural responses in an abnormal environment; for example, bed eating may represent redirection of grazing behaviour in stabled horses without access to a high-fibre forage (Mills et al., 2000). Secondly, the activities may be the stabled horse's attempts to gain some control over its environment; for example, crib biting may reduce arousal in stabled horses (McGreevy and Nicol, 1998a). Thirdly, stereotypic responses may be an indicator of the failure to cope with captivity; for example, oral activities such as crib biting and wind sucking may help regulate stress (McGreevy and Nicol, 1998c) or digestive physiology (Mills and Macleod, 2002), but foals with high levels of these activities have a high incidence of stomach ulcers (Nicol et al., 2002).

3.1. *Social influences on stereotypic behaviour*

Two factors in particular have been associated with the development of stereotypic behaviour in stabled horses: social isolation and the feeding of concentrates without access to high-fibre forage. Traditionally, stabled horses are singly housed for ease of management and have little opportunity for contact with other horses (Mills and Clarke, 2002). Indeed, stereotypic behaviour was thought to be copied between horses so known stereotypers can be unpopular on yards or even visually isolated from other stabled horses. This anecdotal evidence has, however, never been substantiated by controlled experimental studies of the development of stereotypic behaviour and contrasts with the findings of both epidemiological and empirical studies of stereotypy that found that enhancing the horses' social environment actually

reduced the incidence of stereotypy. McGreevy et al. (1995) found that stereotypy was less common on large yards where horses had visual contact with a large number of other horses. The low incidence of stereotypy in these yards may be related to a number of factors (e.g., increased yard activity compared with smaller yards), but within these yards, increased visual contact with other horses was also a factor in lowering risk of stereotypy. In empirical studies, allowing close visual and tactile contact with the neighbouring horse (directly through a grille between stables, as opposed to when the horses happened to have their heads out of the stable door) significantly reduced weaving and nodding relative to the conventional stable (Cooper et al., 2000). The increased close social contact may help explain the low incidence of stereotypy in stall-tied horses, such as those of the household cavalry (Haupt and Ogilvie-Graham, 2002) or pregnant mare urine industries (Flannigan and Stookey, 2002), where there is greater opportunity for social interaction with near neighbours than singly housed or socially isolated stabled horses (Cooper and McGreevy, 2002).

It may, however, be inconvenient or impractical to socially house all horses due to risk of infection, undesirable social interactions or just the cost of maintaining additional horses. A simple alternative may be the use of stable mirrors, which appear to have a similar effect to social contact in both short- (Mills and Davenport, 2002) and long-term (McAfee et al., 2002) studies. Whether horses with mirrors "see" another horse or are merely distracted by the movement is not clear, but whatever the horses see appears to reduce weaving and may offer the individually housed horse with the perception of some choice over its social environment.

3.2. *Influence of feeding practices on stereotypic behaviour*

Stabled horses are often fed high-energy, low-fibre concentrates, as this is a convenient means of providing horses with a finely balanced ration (Davidson and Harris, 2002). However, the horse is naturally a grazer of poorer forages, often spending significant parts of the day feeding, and high-energy feeds require little time to process. In the stabled horse, a number of lines of evidence link stereotypic

patterns of behaviour, such as weaving and crib biting, with the feeding of concentrates (Cooper and Mason, 1998; Nicol, 1999). Firstly, the feeding of high-energy, low-fibre concentrated feeds without access to high-fibre forage is associated with a higher incidence of stereotypic activities in both epidemiological (McGreevy et al., 1995; Nicol, 1999) and experimental studies (Gillham et al., 1994; Johnson et al., 1998). Secondly, the initiation of bouts of stereotypic behaviour has been associated with feeding time. Weaving, for example, has been found commonly to occur prior to receiving a concentrated feed, while oral stereotypies have been described as a common postprandial activity in horses with little fibre (Cooper and McGreevy, 2002). Thirdly, the development of stereotypy and, in particular, oral stereotypies has been associated with the provision of hard feed to foals around the time of weaning (Waters et al., 2002).

Oral activities, such as wood chewing or crib biting, may represent the perseverance of feeding motivation in the face of a relatively small or incomplete meal or attempts to supplement the concentrate feed with additional sources of fibre or bulk. Oral stereotypies are more common in horses without access to forage such as hay at meal times (Willard et al., 1977; McGreevy et al., 1995; Johnson et al., 1998). Providing forage around feeding times significantly reduces the incidence of these activities. Furthermore, other activities frequently described as undesirable by horse owners, such as bed eating, may serve a similar function of allowing horses to express foraging behaviour within the stable environment. Housing horses on beddings that increase opportunity for expression of foraging behaviour, such as straw, reduce the incidence of oral stereotypies compared with non-straw bedding (McGreevy et al., 1995; Mills et al., 2000).

3.3. Reducing performance of stereotypic behaviours

Stereotypic activities are often treated by seeking to prevent performance of the activity (e.g., by using anti-weaving grilles or anti-cribbing collars) rather than by seeking to identify and resolve the underlying environmental challenges (McGreevy and Nicol, 1998a; Cooper and McGreevy, 2002). Prevention of stereotypy per se may lead to two problems. The first is that the horses may persist with the activity but in a

modified form. For example, weaving horses may continue to weave but within the stable if anti-weaving grilles are placed on the stable door (McBride and Cuddeford, 2001), and cribbing collars actually increase the number of bouts of crib biting (McGreevy and Nicol, 1998b). The second problem is that prevention can be distressing to the animals involved. There is good evidence that preventing specific stereotypies causes physiological responses consistent with increased stress, such as raised heart rate and adrenocortical activity. These elevated responses have been found when methods of physical prevention are used, such as anti-weaving grilles (McBride and Cuddeford, 2001) and anti-cribbing collars (Lebelt et al., 1998; McBride and Cuddeford, 2001) and even the removal of favoured cribbing surfaces (McGreevy and Nicol, 1998c).

3.4. Is stereotypic behaviour an adaptive response?

Elevated heart rate and corticosteroids and perseverance of the activity in alternative forms suggest that these repetitive activities may have a general adaptive or coping function (Cooper and Nicol, 1993), e.g., by buffering the horse from noxious stimuli or regulating the level of arousal or psychological distress. Although an association between prevention of stereotypic behaviour and increased arousal has been found in the stabled horse (e.g., see Lebelt et al., 1998, McGreevy and Nicol, 1998c, McBride and Cuddeford, 2001), evidence for a general coping function for stereotypic behaviour in stabled horses has been described as weak (Nicol, 1999). The finding that prevention of an activity leads to an increase in distress does not indicate that the activity originally developed as a response to distressing conditions. Instead, it demonstrates that its prevention, once it is part of the animal's behavioural repertoire, is potentially frustrating. One study only has shown more convincing evidence of a closer relationship (McGreevy and Nicol, 1998c) between stereotypic behaviour and a reduction in arousal. In this study, removing cribbing surfaces resulted in elevated corticosteroids except where horses had access to an alternative means of expressing postprandial oral activity, namely, a full hay net.

Rather than having a general coping or stress-buffering function, individual stereotypies may be

associated with specific environmental challenges. For example, oral stereotypies have been suggested to have some form of adaptive function specifically related to digestion (Nicol, 1999). It has been known for some time that the feeding of concentrate diets (Rowe et al., 1994) and periods of food deprivation increase gastric acidity to harmful levels that can result in rapid ulceration (Murray and Eichorn, 1996). High-concentrate diets also alter caecal fermentation and increase caecal acidity (Willard et al., 1977). Early signs of abnormal wood chewing and stable biting were higher in horses fed with a predominantly concentrate diet than horses that received hay (Waters et al., 2002). However, this did not remain true if the horses fed with concentrates were given an additional supplement, virginiamycin, which suppresses lactic acid production in the hindgut and increases hindgut pH (Johnson et al., 1998). These lines of evidence suggest that crib biting may function to reduce acidity of the digestive tract. The exact mechanism by which crib biting could reduce the acidity of the digestive tract is not known, but it has been suggested that this activity may result in increased salivary flow (Nicol, 1999).

Finally, although these responses may be an attempt to solve environmental deficiencies, their continued expression does not mean they are wholly successful compared with related activities that might be performed in the wild, and that the horse's welfare is ensured. Endoscopic investigation of yearlings with a high incidence of wind sucking and crib biting revealed high levels of gut damage in these animals, including lesions, ulceration and damaged mucosal tissue despite the oral activities (Nicol et al., 2002). This finding suggests that the animals are not successfully coping. Under these circumstances, further intervention may be required, such as provision of a more appropriate (higher fibre) diet or dietary supplements, such as antiacids, to aid gut function under such extreme nutritional challenge (Nicol et al., 2002; Mills and Macleod, 2002).

4. Summary and further work

While free-ranging horses are successful in a range of natural environments from semi-arid to sub-arctic habitats, captive horses with less control over

their environment, level of activity and diet may frequently be exposed to environmental conditions beyond their ability to cope. Under these conditions, a number of activities may arise that are indicative of specific environmental deficiencies, in particular, stereotypic behaviour such as crib biting and weaving. Physiological and behavioural studies of the causes and effects of stereotypic behaviour suggest that inappropriate diet and lack of social contact are primary causes of stereotypy, and that prevention of the behaviours per se without addressing their underlying causes can lead to distress. Instead, by understanding the original functions of certain stereotypic behaviours, these studies may help to suggest changes to management practices that reduce the behaviours without adversely affecting the horse's quality of life.

Thus far, the evidence that stereotypic activities represent an adaptive response is appealing but circumstantial, as studies have tended to investigate horses once the behaviours have become established rather than during their development. More convincing evidence would be provided by prospective studies that followed the development of the activity and associated changes in physiological state. These have begun to be carried out at least for environmental risk factors. For example, Waters et al. (2002) found that weaning practice predisposes horses to certain stereotypies, and specifically, that providing concentrates at weaning is a significant risk factor. However, studies should, wherever possible, include monitoring of the animals' health and physiological status. For instance, a recent study found that antiacid supplements appear to both reduce cribbing and improve the condition of the stomach lining (Nicol et al., 2002). This type of study illustrates the importance of using an inclusive approach to ensure that all consequences of a behaviour or management practice on the welfare of the animal have been assessed.

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