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Why It Is Important to Understand Animal Behavior

Joy Mench

INTRODUCTION

"Animals should be housed with a goal of maximizing species-specific behaviors and minimizing stress-induced behaviors" (NRC 1996, p 22)—a laudable goal, but can it be achieved? The answer is perhaps, but doing so will necessitate addressing some difficult questions. How do we maximize behaviors in an environment that is so different from the one in which the animal evolved its species-typical behaviors? Should the animal be allowed to perform all of its species-typical behaviors or only certain ones? If the latter, how do we choose which ones? How can we recognize and minimize stress-induced behaviors?

Although people have long been fascinated by the behavior of animals, the formal discipline of animal behavior—ethology—is actually relatively new, dating to the work of Konrad Lorenz in Austria in the 1930s. Application of ethological principles and methods to the study of animal welfare is an even newer endeavor, of course, and one that has generated a great deal of stimulating discussion and controversy during its short history. In this paper, I provide an overview of the development of behavioral approaches to the study of animal welfare. I then discuss some reasons that behaviors are important to animals and describe how an understanding of behavior can be useful when designing housing environments for laboratory animals.

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BEHAVIORAL APPROACHES TO THE STUDY OF WELFARE

Background

The report on intensive farming practices authored by the Brambell committee (1965) was probably the first published document to emphasize the importance of behavior in assessing animal welfare. This committee was established by the British government after the public outcry following publication of Ruth Harrison's exposé of what she referred to as "factory farming" methods in *Animal Machines* (1964). After hearing testimony and reviewing farming practices in Europe, the members of the committee wrote (Brambell 1965, p 10):

> The scientific evidence bearing on the sensations and sufferings of animals is derived from anatomy and physiology on the one hand and from ethology, the science of human behavior, on the other ... we have been impressed by the evidence to be derived from the study of the behaviour of the animal. We consider that this is a field of scientific research in relation to animal husbandry which has not attracted the attention which it deserves and that opportunities should be sought to encourage its development.

They further concluded that animals had behavioral needs that could not be satisfied in barren, restrictive environments, and that not providing for those needs was likely to cause suffering, ideas that have proven to be very influential in shaping ethological research on animal welfare.

In an appendix to the Brambell report, the eminent zoologist W. H. Thorpe argued that welfare is promoted when animals are able to perform the activities that most closely resemble the behavioral repertoire of their free-ranging conspecifics. However, this idea soon fell into disfavor among many scientists studying animal welfare (Dawkins 1980). Fraser (1989), for example, discussed the limitations of using the normal behavioral repertoire as the baseline for ensuring welfare with reference to 3 normal behaviors in swine: the distress calls given by piglets when they are separated from their mothers; nest building by sows before parturition; and wallowing, which is a thermoregulatory behavior shown only under hot conditions. Fraser pointed out that a pig's natural behavioral repertoire consists of things that the pig really does not want to do (such as give distress calls), wants to do (such as build a nest), and wants to do but only when conditions require it (such as wallow).

The 3 behaviors described above obviously have different implications for welfare. Providing a pregnant sow kept in a temperature-controlled environment with a wallow would do little to improve her welfare, whereas giving her nest-building material might improve her welfare a great deal. Placing piglets in a situation in which they give distress calls, however, would actually reduce their welfare. Thus, to assess the welfare significance of particular behaviors, it is important to have an understanding of what causes the behavior to occur in the first place.

Motivation and Welfare

Many factors can motivate the performance of behaviors, and a variety of models have been proposed in an attempt to explain how motivational systems work (Jensen and Toates 1993; Toates 1986). One approach to studying motivation has been the attempt to determine the relative importance of internal and external factors in causing particular behaviors (for example, Hughes 1988). Some behaviors are classified as being motivated primarily by factors external to the animal, exemplified by thermoregulatory behaviors like wallowing in pigs and antipredator behaviors in prey species. Other behaviors, like food searching when hungry, appear to be largely internally motivated. Yet other behaviors are elicited by complex interplay between both internal and external factors. Mating behavior, for example, is motivated by hormonal state, which may in turn depend on seasonal and other environmental factors as well as the accessibility and readiness of appropriate sexual partners. Cues from one partner to the other during courtship can further influence the hormonal states and behavior of the courting pair.

The study of motivation has been very important in applied ethology because of its link to the Brambell committee's ideas about behavioral needs. Behavioral needs are generally conceptualized as those behaviors that the animal must perform regardless of environmental circumstances, that is, primarily internally motivated behaviors that may occur even in the absence of appropriate external stimulation, although sometimes in an aberrant form. Hens kept in cages without litter material, for example, will still perform dustbathing behaviors, although the movements are somewhat abnormal and the dustbathing episode is short compared with a normal dustbathing episode (Vestergaard 1980). Behaviors of this type are called vacuum activities (because they occur "in a vacuum," so to speak). Another form these behaviors can take is to become stereotyped. Many oral stereotypies, for instance, have been shown to be associated with the lack of opportunity to perform particular components of feeding behavior, including foraging (Bayne and others 1991; Redbo and Norblad 1997; Rushen and others 1993).

A thorny question remains, however: Is the performance of an aberrant behavior, or not meeting a behavioral need, linked to "suffering" (hereafter referred to as distress) as the Brambell committee claimed? Duncan (1978a) argued that independent verification was necessary to demonstrate that unusual or inappropriate behaviors indicated reduced welfare. One common approach to providing such verification has been to measure physiological (including immunological) parameters associated with stress and then to attempt to correlate those parameters with abnormal behaviors or responses to behavioral restriction. However, physiological measures also have many limitations, and it has generally proven difficult to interpret their significance as indicators of welfare (Dawkins 1980; Mason and Mendl 1993; Rushen and de Passillé 1992). The answer to the question about suffering is therefore still elusive, as can be demonstrated by considering research on abnormal behaviors.

Abnormal Behaviors

In the laboratory setting, abnormal behaviors are often used as the benchmark of poor housing conditions and the need for environmental enrichment. Behaviors that cause injury to either the initiator (self-mutilation) or the recipient (cannibalism) clearly have a negative effect on the welfare of the individual sustaining the injury. However, no consistent relationship has been demonstrated between noninjurious abnormal behaviors, particularly stereotypies, and other measures of reduced welfare (Lawrence and Rushen 1993; Mason 1991; Mench and Mason 1997).

Stereotypies are sometimes, but not always, linked to physiological changes indicative of stress; and in fact, the performance of stereotypies sometimes appears to be rewarding or to reduce stress. Although abnormal behaviors often appear to arise from frustrated motivation, they may also be caused by factors that are not directly related to a poor environment, such as pathology or neurological predisposition. Most puzzling is that established stereotypies may also persist even when animals are placed in enriched environments. Has the enriched environment failed to improve the animal's welfare? Mason (1991) suggests instead that stereotypies may be as much "scars" of past experience as they are indicators of current frustration or environmental inadequacy. Since many stereotypies can be prevented from forming by altering the animal's environmental conditions, there is widespread agreement that appropriate steps should be taken to accomplish this (Duncan and others 1993).

Preference Testing and Demand Curves

Another way in which behavior has been used to provide information about welfare is in studies giving animals choices and opportunities to express preferences (Dawkins 1980). In a pioneering study of animal preferences, Hughes and Black (1973) decided to test a recommendation made by the Brambell committee—that laying hens should be kept in cages with floors made of rectangular metal mesh, rather than fine-gauge "chicken wire," because the latter sags and the hen's foot is not well adapted to grip it comfortably. Hughes and Black gave hens a choice of 4 different types of flooring including chicken wire, 2 types of rectangular mesh, and perforated metal. The hens obviously viewed the situation somewhat differently than did the Brambell Committee; they chose the chicken wire in preference to the other floors, and subsequent visual inspection showed that the chicken wire in fact provided the best support for their feet. Preference testing of this type has now been used widely in studies of animal welfare, including assessing preferences shown for cage height, light intensity, flooring, bedding material, and enrichment devices by rats (Blom and others 1995, 1996; Chmiel and Noonan 1996; Manser and others 1995; van de Weerd and others 1996), sleeping locations by mice (Sherwin 1996), flooring and social companions by hamsters (Arnold and Estep 1990, 1994), and social companions by rabbits (Held and others 1995).

Cautions have been raised about the use and interpretation of preference testing (Dawkins 1980; Duncan 1978b). Preferences can be shaped by many factors, including genetics, previous experience, and the choices offered and testing methods used. Short-term choices may not correspond well to long-term welfare, since animals (like humans) may choose things that are immediately rewarding but are not necessarily best for them in the long term. An awareness of these problems has led to a rapid evolution of preference testing toward asking more precise questions and taking more comprehensive measures (Fraser and others 1993); and preference testing is now widely considered to be a useful tool, particularly for evaluating specific aspects of the environment like flooring, temperature, and lighting.

One enduring criticism leveled against preference testing, however, is that it fails to distinguish between important choices and not-so-important ones—between so-called "luxuries" and "necessities." Dawkins (1990) developed a model that she suggested could address this concern by allowing the strength of the motivation underlying particular choices to be determined. Her "consumer demand" model is derived from economic theory and involves requiring animals to pay some kind of cost to acquire commodities. For instance, a hen might have to peck a key or push through a barrier to gain access to a nestbox or dustbath. The amount of key pecking or barrier pushing she is willing to do can be compared with the amount she is willing to do to obtain a commodity known to be important to her, such as food. Priority can then be given to providing opportunities for animals to perform those behaviors for which they show a strong demand (that is, needs).

Dawkins argues that an animal will work the most for things that ensure its fitness or are perceived to be important in ensuring its fitness. This is an important concept because it emphasizes that domesticated and purpose-bred animals may continue to behave in ways shaped by their evolutionary history, even if those behaviors are not necessarily important for (or are sometimes even detrimental to) their survival or fitness in captivity. In fact, most behavioral changes accompanying domestication are qualitative rather than quantitative, that is, they result in changes in the frequency, rather than the elimination, of behaviors from the species-typical repertoire (Price 1984).

A number of problems have been reported (including by Dawkins herself) concerning application of the consumer demand model (see Dawkins 1990 and commentaries; Houston 1997), although these problems are largely methodological in nature. A broader issue, however, relates to the underlying assumptions of the model and, indeed, of the whole concept of behavioral needs. Jensen and Toates (1993) conclude that it is almost impossible to separate behaviors into needs and nonneeds. Using a series of examples, they demonstrate that both internal and external stimuli contribute to the motivation of even seemingly simple behaviors and that different circumstances can cause a particular type of stimulus to assume more or less importance in causing the behavior. The powerful effects that an external stimulus can have, even on a behavior that we think of as largely internally motivated, is unfortunately well-known to most of us. For example, consider how we respond to a particularly tempting desert even after a very filling meal! Accordingly, Jensen and Toates (1993) argue that behavioral needs will be situation-specific rather than generally applicable and that trying to devise a catalog of a particular species' behavioral needs is futile. Thus we come full circle: If we are not able to identify behavioral needs, then what is the relationship between species-typical behaviors and welfare?

WHY IS BEHAVIOR IMPORTANT?

It is worth remembering that behavior is what animals <u>do</u> to interact with, respond to, and control their environment. Behavior is generally the animal's "first line of defense" in response to environmental change. As such, careful observations of behavior can provide us with a great deal of information about animals' requirements, preferences and dislikes, and internal states (Mench and Mason 1997), provided that our interpretation of those observations is firmly grounded in a knowledge of species-typical behavior patterns.

An approach to management or housing design that focuses primarily on behavioral needs is too narrow (Mench 1998b) and does not adequately consider the beneficial effects a behavior can have on welfare even when that behavior might not be defined typically as a need. I suggest that we reconsider simple behavioral preferences, and indeed species-specific behaviors in general, and identify the *consequences* for an animal performing particular behaviors. The association between potential welfare benefits and an animal's performance of certain behaviors is further discussed below. This, however, is an area in which much additional research is needed, particularly for laboratory animals.

Maintaining Physical Health or Physiological Normality

The performance of certain behaviors can lead to improvements in physical health. The beneficial effects of exercise on humans are well known, and similar effects can be observed in animals given the opportunity to engage in species-typical patterns of locomotion. For example, dairy cows walked daily have fewer leg problems, including noninfectious leg and hoof disorders, as well as lower incidence of mastitis, bloat, and calving-related disorders, than cows kept in tie stalls (Gustafson 1993). Captive birds whose movement is restricted tend to develop osteoporosis and osteoarthritis (Fedducia 1991; Knowles and Broom 1990), and 5% of caged laying hens are found to have old, healed bone breaks at necropsy (Gregory and Wilkins 1989). Providing the opportunity for perching behavior, however, can help to reduce bone breakage. Caged hens given raised perches have greater leg-bone and wing-bone strength (Hughes and Appleby 1989), as well as better foot health, than hens from cages without perches.

Less obvious, perhaps, are the effects that performing behaviors can have on normal physiological functioning. In studying the welfare of early-weaned calves, de Passillé and others (1993) found that the suckling reflex was stimulated when the calves were fed even small quantities of milk and that the reflex persisted for 10 min after intake. If the calves were allowed to suck a nonnutritive ("dry") teat after their milk meal, production of digestive hormones, including CCK and insulin, was increased. Suckling behavior itself, then, has beneficial effects on digestive physiology in calves.

Studies like these have important implications, not only for animal welfare but also for the outcome and interpretation of biomedical research projects in which animals are used as models. As Valzelli (1973) demonstrated, "a mouse is not a mouse is not a mouse." Socially isolated mice differ from group-housed mice not only behaviorally, but also in their immunological responses, hormone levels, brain neurochemistry, learning ability, pain thresholds, and sensitivity to drugs.

Behavior can thus influence research findings, sometimes in unforeseen ways. Capitanio and Lerche (forthcoming) carried out a retrospective analysis of the effects of different variables, including medical history, housing, demographics, and contents of the inoculum, on the survival of rhesus monkeys experimentally infected with simian immunodeficiency virus. After analyzing colony data from 4 regional primate research centers, they found that housing had a significant effect on the monkeys' ability to survive. Housing relocations and social separations both during the 30-day period after infection and the 90-day period before it were associated with decreased survival, as was grouping during the period after infection. Some of the differences in survivability were dramatic—for example, all of the monkeys who were relocated several times shortly before or after inoculation died within 600 days after infection, even though 40% of the monkeys that had been maintained in stable social groups were still alive.

Preventing or Reducing Illness, Fear, Stress, Pain, or Tension

Behaviors can also be important in reducing illness, pain, fear, stress, or tension. If possible, animals will remove themselves from a fear-producing stimulus by fleeing or seeking cover (or will sometimes attempt to escape detection or injury by becoming immobile). Sick animals show a number of behavioral changes, including anorexia, sleepiness, depression, and a reduction in grooming activity, which help to conserve energy and thus facilitate healing (Hart 1988).

Similarly, animals use behavioral mechanisms to deal with short-term stressors like social interactions. Macaques from a stable social group subjected to a brief period of crowding, for example, avoid conflict by reducing their level of activity (Aureli, and others 1995). Mutual grooming activity similarly reduces stress and tension among socially interacting primates (Boccia and others 1989; Schino and others 1988) and is associated with the release of endogenous opioids (Keverne and others 1989). Social companionship and the ability to engage in social behavior, even aggressive behavior, can also have stress-buffering effects. Rhesus monkeys exposed to novelty show attenuated cortisol responses and less fearful behavior if a familiar social companion is present (Hennessy 1984), and rats that can interact aggressively with another rat during exposure to shock have lower stress levels (Conner and others 1971).

All of the foregoing are examples of behaviors or behavioral changes that are of relatively short-term benefit. However, the performance of behaviors can also have longer-term consequences for the animal. Many studies have shown that providing an enriched or complex environment for the animal, particularly early in life, has far-reaching effects. In a study by Chamove (1989), for example, standard laboratory mouse cages were modified by dividing them into 5 to 9 compartments using plastic sheets. The mice showed a preference for complex cages over the standard cages, and cage partitioning led to increased burrowing activity. In addition, mice from the partitioned cages displayed evidence of reduced stress and fear responses, including greater weight gains after weaning, lower adrenal gland weights, and lower fear scores in 2 standard tests, the open field and emergence test. Thus, although the cage modification was relatively simple, the increased behavioral opportunities afforded the mice had striking effects not only on their behavior, but also on their physiology.

Providing Pleasure, Comfort, or Satisfaction

Most animal welfare research has focused on identifying and minimizing causes of suffering. However, behaviors that contribute to animals' pleasure, comfort, or satisfaction have received comparatively little research attention, although they are widely recognized as important components of human well-being. Through surveys, Meyers and Diener (1995) identified a number of elements that contribute to life satisfaction in humans. These include a sense of control, meaningful social relationships, challenge, and active engagement.

Studies with animals tend to confirm the importance of these factors. Animals able to exercise some behavioral control over their environment show attenuated responses to a stressor compared with animals having no control (Weiss 1972). Although some effects of conspecific social interactions are described above, research on affiliative and social play behaviors is lacking and greatly needed for most laboratory animal species, particularly nonprimate species. Nevertheless, social relationships with human caretakers have been shown to have positive behavioral, physiological, and immunological effects for several species (Davis and Balfour 1992; Hemsworth and others 1993).

Animal preferences provide information about the importance of engagement and challenge. Unless they are quite hungry, animals of many species prefer to work for food rather than eat freely available food, a phenomenon known as contrafreeloading (Inglis and others 1997). Many animals also show a preference for exploring novel environments and objects, even when those environments or objects are not directly associated with needed resources (Mench 1998a). Both contrafreeloading and exploratory behavior have an information-gathering function that is likely to be adaptive under natural conditions, but even in captivity these behaviors are still preferred and can be assumed to have reward value for the animal. Lack of active engagement has been implicated as a primary cause of boredom, depression, and anxiety in animals (Wemelsfelder 1990). Zoo researchers have been particularly innovative in designing environmental features that increase the engagement and control that animals have, even in otherwise restricted enclosures (Markowitz 1990).

Behavior As an Indicator

Behavior has another important function: providing information to human caretakers about the welfare of the animal (for example, Manser 1992). As noted above, however, thorough observation and a sound knowledge of species-typical, and often individual-specific, behavioral patterns are required to interpret this information. Although behaviors are widely used as indicators of pain or illness in laboratory animals (Hart 1988; Morton and Griffiths 1985), crude measures of behavior may fail to correlate well with other measures of pain or distress (Conzemius and others 1997). Nevertheless, well-designed experimental studies can provide information about which behaviors are valid indicators of pain or distress, and even the degree of pain or distress experienced by the animal.

In social species, vocalizations and other social signals may well provide one of the more sensitive indicators, since a function of these signals is to enlist aid from other members of the social group. Weary and Fraser (1995) removed piglets from the sow before or after they were fed and placed them in an adjacent room. Unfed piglets, and also lightweight piglets that were not thriving as well as their littermates, gave more separation calls, and calls that were louder and of greater amplitude, than did fed or thriving piglets. Call rate and amplitude can also be used to assess the distress and pain associated with each of the components of a surgical procedure like castration, from handling through severing the spermatic cord (Weary and others 1998).

DESIGNING HOUSING ENVIRONMENTS BASED ON BEHAVIOR

Animal behavior is rarely given a great deal of consideration in the design of housing systems and equipment, even though behaviorally inappropriate design can lead to injury and other welfare problems (NRAES 1995). Taylor (1995) evaluated various commercially available sow feeders and found that they differed widely in the ease with which sows could feed from them and the number of facial and dental injuries sustained by the sows while feeding. Using static and kinematic studies of sow feeding behavior, Taylor discovered that some feeders were simply not designed to properly accommodate a sow's head shape, space needs, and movement patterns during feeding. The design changes required to better accommodate normal behaviors are sometimes quite simple. Orienting the front bars of laying hen cages horizontally rather than vertically, for example, allows the hens to change feeding location more easily and decreases the likelihood that they will be trapped between the cage bars (Tauson 1985).

An understanding of behavior is also critical to effective environmental enrichment programs. Because animals will not use enrichment devices and enriched environments unless those devices and environments are behaviorally relevant to them, irrelevant enrichments will not help in achieving the goal of maximizing normal behaviors and minimizing stress-induced behaviors (Mench 1998a; Newberry 1995). Effective enrichment often requires a detailed analysis of both patterns of behavior and causes of abnormal behaviors.

An excellent example of this type of analysis is provided by a recent study of Mongolian gerbils (Wiedenmayer 1997).

In the wild, gerbils live in a burrow system they have excavated in sand. Young gerbils housed in standard laboratory cages first begin to dig at the bedding in their cages when their eyes open, but the digging soon becomes stereotyped and directed at the edges of the cage rather than the bedding. In an attempt to learn the actual cause of this stereotyped digging, Wiedenmayer attached to the laboratory cage either a cage full of sand or an excavated burrow (modeled after a wild gerbil burrow). Young gerbils given access to only the sand, which was too dry for them to actually excavate, still developed stereotyped digging. In contrast, those given access to the burrow did not dig, demonstrating that it was the lack of the burrow itself, not the opportunity to dig the burrow, that caused the stereotyped digging. Wiedenmayer then tested the gerbils' response to artificial burrows—a Plexiglas chamber attached to the cage by a tube, simulating the tunnel that leads into the gerbil's normal burrow. The tunnel was the critical feature. Gerbils given only the chamber developed stereotyped digging, whereas those given the tunnel did not.

Determining which components of particular behaviors are most important to different species of animals is not intuitively obvious but requires careful study. Although the gerbils needed only the endpoint of the behavior (the burrow), in some cases performing the actual behavior is also important. Hens given a preformed nest that they had constructed at an earlier time will nevertheless repeat their nest-building behaviors before egglaying (Hughes and others 1989).

Behavior can also be used as the basis for more sweeping environmental design. For several years, Stolba and Wood-Gush (1984) observed the behavior of pigs in a seminatural environment and then designed a housing system that accommodated as many of the natural behaviors of the pigs as possible, including rooting, rubbing/marking, sheltering, nesting, and defecating in defined areas. The system also allowed the pigs considerable freedom in selecting or avoiding particular social companions and was based on a group size that was typically chosen by the pigs under seminatural conditions. Although not widely adopted because of certain economic constraints (Edwards 1995), the system represents an intriguing attempt to use behavior as the basis for designing a housing system rather than simply providing behavioral opportunities as "add-ons" to an already established system. This approach, which obviously requires a detailed knowledge of species-typical behaviors obtained by observing animals in the wild (or in the most naturalistic environment possible), has been used in zoos (Seidensticker and Doherty 1996) more than in agricultural or laboratory settings.

SUMMARY

Ultimately, the answers to the questions posed in the first paragraph of this article will depend on our perception of our ethical obligations to the animals in our care (Sandøe and Simonsen 1992; Tannenbaum 1991). Nevertheless, an understanding of the range, causes, and functions of the species-typical behaviors of animals will be critical underpinnings in addressing laboratory animal welfare issues. Behavior provides a window into the animal's world that, with careful observation and study, can tell us a great deal about what animals do when they are frightened, ill, or in pain, as well as what they prefer and dislike. The application of behavioral principles to the design of laboratory animal housing is an area that merits increased attention from laboratory animal scientists.

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