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Recommended Citation

King, L. A. (2003). Behavioral evaluation of the psychological welfare and environmental requirements of agricultural research animals: Theory, measurement, ethics, and practical implications. *ILAR Journal*, 44(3), 211-221.

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Behavioral Evaluation of the Psychological Welfare and Environmental Requirements of Agricultural Research Animals: Theory, Measurement, Ethics, and Practical Implications

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KEYWORDS

3Rs, agriculture, animal welfare, distress, emotion, environmental enrichment, psychological welfare

ABSTRACT

The welfare of agricultural research animals relies not only on measures of good health but also on the presence of positive emotional states and the absence of aversive or unpleasant subjective states such as fear, frustration, or association with pain. Although subjective states are not inherently observable, their interaction with motivational states can be measured through assessment of motivated behavior, which indicates the priority animals place on obtaining or avoiding specific environmental stimuli and thus allows conclusions regarding the impact of housing, husbandry, and experimental procedures on animal welfare. Preference tests and consumer demand models demonstrate that animal choices are particularly valuable when integrated with other behavioral and physiological measurements. Although descriptive assessments of apparently abnormal behavior such as stereotypies and "vacuum behaviors" provide indications of potentially impoverished environments, they should be used with some caution in drawing welfare conclusions. The development of stereotypies may in some cases be linked to psychiatric dysfunction and reflect underlying neurophysiological impairments, which have implications for the ability to perform flexible behavior and thus the quality of research data provided by this kind of behavioral measurement (e.g., in pharmaceutical research). Environmental modifications, commonly termed "enrichment," can have diverse consequences for cognitive function, physiological responses, health, psychological welfare, and research data. Simple practical modifications of housing, husbandry, and experimental design are suggested to improve the psychological welfare of agricultural research animals in accordance with the principles of refining, reducing, and replacing (the "3Rs"), which underlie US Public Health Service Policy, and prevailing public ethics.

Introduction

Agricultural research animals are used to gain knowledge in many fields of study, ranging from experimental studies relating to human-focused biomedical research and the supply of biomedical and pharmaceutical products to agricultural production research and the study of welfare of food production species. This article provides an outline of the theory and methods by which the psychological welfare and environmental requirements of agricultural animals, such as pigs and poultry,

can be conceptualized in a scientific framework. Subsequent discussions address how the psychological welfare should be considered in the design of experimental research. Although many of the practical considerations focus on the use of animals in studies based outside the laboratory, both theoretical and practical discussions are also relevant for laboratory-based research.

Defining Animal Welfare

Animal welfare is a contentious issue in which judgments are based not solely on scientific evidence but also on philosophical value statements and economic considerations (Duncan and Fraser 1997; Fraser 1997; Stafleu et al. 1996). Consequently, it is important first to define what is addressed when attempting to describe "animal welfare." Welfare involves the prudential value of a life, namely, "how well it is going for the individual whose life it is" (Sumner 1996). This meaning suggests that although agricultural animal welfare will depend on the resources and husbandry provided to the animal, the effect of human actions on animal well-being will be beneficial only if changes positively influence the animal's intrinsic state (Duncan 1998).

Within the scientific and philosophical study of animal welfare, debates continue as to what constitutes an individual animal's welfare. Traditionally, the well-being of agricultural animals has been construed in physical and physiological terms, focused on veterinary concepts of animal health or productivity (discussed in Dawkins 1980). Indeed, some scientists have suggested that an animal's welfare is a concern only when its evolutionary fitness is reduced (Barnard and Hurst 1996); to reflect on Sumner's (1996) definition, an animal's life is not going well if its longevity or reproductive capability is likely to be curtailed. Physiological and physical measures describing damage to the animal may be useful for one or more of the following reasons: (1) They may demonstrate the effects of environmental challenge on health and optimal physiological function; (2) they may reflect an individual's ability to adapt effectively to the current environment; and (3) they may indicate pathological states that are a concern not only for animal welfare but also because they may impinge on research results (Broom and Johnson 1993). Physiological responses to environmental challenge could be determined by genetic design rules, however, in which case behavioral and physiological responses would be essentially a mechanistic process, evolved to reduce hazardous impacts on lifetime reproductive success (Duncan and Fraser 1997). In other words, an animal that had encountered environmental challenge beyond its means of adaptive response would incur detrimental effects on its function, like a car that had traveled too many miles between each oil change, but not necessarily suffer in the process. However, concern is not expressed for the welfare of machines; so why is animal welfare not simply a mechanistic construct?

Subjective Experiences and Distress

The concept of suffering or distress relies explicitly on the ability to experience intrinsic states as pleasant or unpleasant. Subjective emotional states include those associated with pain, illness, and the ability to perform functional behaviors, which gain resources or avoid dangerous stimuli or which allow the animal to cope with environmental challenge, altering its motivational state and leading, for example, to relief (Broom and Johnson 1993; Rolls 1999). Animals are not simply mechanistic rule-based or stimulus-response organisms as historically proposed by behaviorist conceptions (Griffin 1981; Rollin 1990; Rolls 1999). Scientists working on animal emotions and animal welfare propose that agricultural animals such as pigs and poultry (including birds) differ from machines in that as part of their "telos" or nature of being (Rollin 1990), they are cognitive and may experience simple emotional states (Dawkins 1990; Griffin 1981). What is the basis for this claim?

Neurophysiologists and ethologists have proposed that emotions evolved in humans, nonhuman animals, and birds as a mediator of flexible behavior, allowing animals to evaluate perceived stimuli in the environment and produce appropriate, highly flexible behavioral responses. In the unpredictable natural world, flexibility of response would be evolutionarily advantageous, optimizing opportunities to act to achieve proximate goals that, in turn, maximize evolutionary fitness by removing the animal from hazardous stimuli that may lead to death or reduce its ability to reproduce (Dawkins 1990; Fraser and Duncan 1998; Rolls 1999; Wiepkema and Koolhaas 1992). Although behavior toward or away from stimuli could also be determined by simple design rules linking perception of stimuli to reflexive behavior, as in the case of taxis and tropisms, this type of design would support only a limited repertoire of fixed stimulus-behavior interactions and would not allow the kind of flexible responses observed in mammals and birds (Rolls 1999).

Neurophysiological research has shown that emotional processing provides a link between perceived stimuli and behavioral responses (e.g., Rolls 1999). Emotions reflect the positive or negative value of stimuli, which act as rewards or punishments, respectively. A diverse range of stimuli can be evaluated and linked to the processing of behavioral decision-making, with the results of evaluation providing an informational basis for selecting between diverse behavioral responses (Cardinal et al. 2002; Rolls 1999, 2000). Furthermore, neurophysiological evidence has shown that many animal species possess neural mechanisms that are homologous to human processing of emotions (Cheng et al. 1999; Rolls 1999). Although it is not proposed that all animals experience the same complex quality of emotion as humans (e.g., grief and jealousy, which require extensive higher-order cognitive processing), fundamental emotions such as fear, anxiety, and frustration may be possible (Dawkins 1998; Fraser and Duncan 1998).

Although the neurophysiological mechanisms underlying animal emotion have begun to be understood, how can scientific observations of subjective emotional states be made, and how can we identify what aspects of husbandry or resources impinge on animals' psychological welfare? Subjective experiences of pleasure or distress are not inherently observable and therefore are not directly open to scientific measurement. However, emotional states influence motivational mechanisms, which are in turn reflected in the extent and type of flexible behavioral responses (Dawkins 1990; Duncan 1998). Operationally, motivated behavior occurs when "an animal . . . will perform an arbitrary operant [instrumental] response to obtain a reward or to escape from or avoid a punishment" (Rolls 1999, p. 3). In other words, the animal will demonstrate its priorities by "voting with its feet" (Dawkins 1990). Behavioral measures of motivation provide an observable correlate of the subjective state and enable us to quantify the importance the animal places on gaining or avoiding particular stimuli.

Measuring Animal Priorities

Preference Test

The most simple measure of an animal's choice is the preference test, which determines an animal's relative choice for different resources. Preference tests are valuable as a first step in understanding animal priorities because they are practical, relatively easy to perform, and highly externally valid when animals are tested in environments that mirror the animal's usual housing (Fraser and Matthews 1997). These tests have been used widely in animal production species to determine whether animals have a requirement for particular resources in their captive environment, sometimes with counterintuitive results. For example, hens have been shown to prefer certain flooring types that were not previously recommended by scientific and animal husbandry consultants, to alter their behavior based on cage dimensions, and to prefer outdoor areas to cages, but only after they were afforded opportunities to

experience an outdoor environment (Dawkins 1977; Hughes and Black 1973; Nicol 1986). When partnered with simultaneous behavioral studies, preference tests can provide a good indication of how the animal utilizes its environment (e.g., Nicol 1986).

There are some limitations of preference tests, however, with respect to their ability to indicate an animal's environmental requirements. First, it is unclear whether the animal's choices, influenced by immediate stimuli, reflect its long-term priorities (Duncan and Fraser 1997). Second, in both the complex evolutionary environment and the modern laboratory and production environments, animals rarely have "one-zero" decision-making options but rather have a range of potentially interacting social and physical stimuli such as conspecifics and food resources. Many methodological problems can be overcome by creating "closed economies," where the animal lives long-term in an environment that includes all of the resources that are being tested with no access to resources outside the test arena (e.g., Kristensen 2000). However, it should be noted that preference tests inform about animal choices, rather than priorities (Duncan 1978). Therefore, it is not clear whether the animal is choosing between two valued commodities or is choosing the "lesser of two evils" (Duncan 1992, 2000). If indeed the goal is to reduce or prevent distress or poor welfare caused by housing or husbandry--fulfilling the principles of refinement, reduction, and replacement (the 3Rs¹; Russell and Burch 1959)--it is necessary to have a method for evaluating the importance of resources from the animal's perspective.

Consumer Demand

Consumer demand research is a promising and relatively recent development in the assessment of animal welfare, which focuses on measuring the strength of an animal's motivation to gain particular resources. This field of research uses techniques adapted from human microeconomics, measuring demand for resources by determining how the animal's behavior changes when increasing costs are imposed on access or utilization (Mason et al. 2001). Demand studies can demonstrate the extent to which an animal requires a resource, or how important it is for the animal to avoid or escape from a stimulus such as a stockperson, a piece of equipment, or an environment where a particular procedure takes place (Mason et al. 2001, Matthews and Ladewig 1994; Petherick and Rutter 1990; discussed further in Fraser and Matthews 1997). Knowledge of animal priorities is valuable for animal welfare because animals may experience positive emotional states when resources they require are provided or, conversely, experience unpleasant states such as frustration when resources related to their performance of intrinsically motivated behaviors are unavailable (Dawkins 1990). They may experience anxiety in environments associated with prior unpleasant experiences, fear when exposed to aversive stimuli (Rolls 1999), or frustration in the absence of a valued resource (Savory et al. 1992, 1993).

In consumer demand studies, the animal's priorities are indicated by the extent to which it maintains a behavioral response in the face of increasing costs. The currency of cost can vary in terms of the proportion of available time used in interacting with the resource, the physical amount of work required to gain the resource, such as pushing a weight or pressing a key, or the extent of an aversive stimulus endured to gain the resource (e.g., Cooper and Appleby 2003; MacCaluim et al. 2003; Mason et al. 2001; Rushen 1986). The choice of cost depends on the species and resources studied because costs have different biological relevance (Dawkins and Beardsley 1986).

Demand studies are powerful indicators of animal priorities, and they may be used to determine the relative importance of a wide range of resources (e.g., Mason et al. 2001). They can also reveal states of distress that may not be obvious in watching individual, group, or flock behavior (Dawkins 1980, 1999). For example, it has been shown that broiler breeder hens reared on a restricted feed ration, similar to those provided in commercial husbandry, work more than three times as hard to gain food compared with

hens reared with ad libitum feed access but then completely deprived of food for 72 hr (Savory et al. 1993). Their behavior suggests a state of extreme frustration of feeding motivation, with a potential for an associated subjective state of hunger, which would not otherwise be obvious from observations of "everyday" behavior.

Demand and preference studies have been used widely to uncover animal priorities. For example, they have been used to assess feeding motivation in sheep (Jackson et al. 1999), broiler breeders (Savory and Lariviere 2000), and pigs (Bergeron et al. 2000; Lawrence et al. 1988, 1989); to study the influence of experience on the importance of nesting behavior in hens (Cooper and Appleby 1995); to evaluate calves' requirements for social contact (Holm et al. 2002); to determine which resources laboratory-housed mice value to facilitate locomotion and to study possible benefits of extra cage space (Sherwin 1998; Sherwin and Nicol 1997); to identify the environmental requirements of hens for litter materials (Gunnarsson et al. 2000); to identify the requirements of hens for the performance of dust bathing behavior (Widowski and Duncan 2000), the potential aversiveness of sounds (McAdie et al. 1993), and preferences for ultraviolet (UV1) light spectra (Moinard and Sherwin 1999).

Although demand studies utilize complex apparatus and require careful consideration of methodology, lengthy animal training periods, and extensive time (Kirkden 2003; Mason et al. 1997, 1998a,b; Petherick and Rutter 1990; Sherwin and Nicol 1998), they are currently among the most promising indicators of the behavioral and resource requirements of captive animals (Mendl 2001). They are particularly useful when paired with other measures, for example, physiological indicators such as cortisol production, a hormone often used as a correlate of the subjective experience of stress (e.g., Mason et al. 2001). Indeed, it may only be possible to make welfare-oriented interpretations of physiological measures such as cortisol or corticosterone production with this associated knowledge of behavior or animal priorities because similar physiological responses may be associated with both positive and negative emotional states, or may be produced as an artifact of behavioral changes due to environmental modifications, such as the extent of locomotory activity (Dawkins 1998, 1999 and Rushen 1991, for detailed discussions).

Behavior in Research Environments: Implications for Welfare

Other behaviors may shed light on an animal's psychological welfare and may be useful in the research environment because they may occur in the animal's home pen and are observable without recourse to complex experimental studies. Welfare problems can be identified by the existence and extent of behaviors such as aggressive interactions that may lead to injury or other behaviors that may indirectly indicate frustration or other forms of distress. In the text below, the welfare implications that can be drawn from behavioral measures are assessed in an effort to identify the strengths and limitations of using abnormal behavior or the diversity of behavioral repertoire as indicators of psychological welfare.

Natural Behavior Repertoire and Welfare

Evolved Behavioral Strategies

Functional perspectives of behavior propose that animals have evolved behavioral strategies, which improve their abilities to gain resources, avoid hazards, and maximize survival and reproductive capabilities in the evolutionary environment (Dawkins 1998). Does this mean that animals need to perform all behaviors seen in the wild, or that their welfare is always good within the natural environment? It appears that this is not the case. In the evolutionary environment, animals experience disease and injury and may be subject to predation, all of which reduce welfare (Dawkins 1990). Goal-directed behavior may be frustrated from achieving its end-point due to lack of resources, as in periods of food

shortage. Although the performance of a wide behavioral repertoire has been proposed as an indicator of good welfare, the performance of aspects of the wild or natural behavioral repertoire, such as escape and frustration-related behaviors, clearly does not reflect an animal having a good state of psychological welfare (Dawkins 1999).

Role of Stimuli

Do animals need to perform particular behaviors? An animal may not suffer if it is allowed to attain its goal, even though it is unable to perform the appropriate appetitive behavior. The "need" to perform behavior arises from the relative contribution of intrinsic versus extrinsic stimuli in the control of behavior, or the consequences of their interaction (Duncan 1998; Jensen and Toates 1993). When behavior is influenced primarily by extrinsic stimuli, there may be little requirement to perform behavior if these stimuli are absent in the captive environment. Behaviors that are primarily internally motivated may be of high priority to the animal, however, even when environmental stimuli are not present, because motivation to perform the behavior arises independently of environmental factors (Duncan 1998).

Behaviors performed in the absence of eliciting environmental stimuli have been termed "vacuum behaviors" (Broom and Johnson 1993). This term implies that the behavior is strongly intrinsically motivated and that a particular resource is required for the performance of the behavior, which is absent in the environment. Vacuum behaviors closely resemble normal behavioral sequences. For example, hens housed on litter perform dust bathing, a series of sweeping and shaking movements, to maintain feather quality (van Liere and Bokma 1987), whereas hens housed in wire cages, with no litter substrate to facilitate feather lipid removal, continue to perform dust bathing sequences in the base of the cage (Lindberg and Nicol 1997). Performance of behavior in the absence of eliciting stimuli might suggest a strong intrinsic motivation to perform the behavior, so the lack of litter potentially constitutes behavioral deprivation (Duncan 1998). Indeed, independent evidence suggests that dust bathing is highly motivated: Hens deprived of litter show rebound, or excessive performance of dust bathing, when subsequently provided with a substrate (Norgaard-Nielsen 1997). Caged hens also substitute other resources for litter, for example, flicking food particles onto their head and back (noted in Dawkins 1998). However, it is not clear whether the inability to perform behaviors due to the absence of eliciting stimuli causes suffering, without independent evidence of specific motivation to obtain the litter substrate to perform the behavior.

Other behaviors may indicate that an animal is motivated to obtain a resource that is not available in the captive environment. Behaviors that would normally be performed toward particular substrates may be directed toward other resources, such as broiler breeders pecking objects such as drinkers and the pen wall, or crated sows mouthing metal pen bars (e.g., Kostal et al. 1992; Rushen 1985). At first glance, it may seem abnormal for a clearly functional behavior to be directed toward an inappropriate resource. However, again these resources may be suitable substrates for the performance of the behavior, or may have stimulus qualities that are perceived by the animal or bird as the target of functional behavior. Unless independent experimental evidence demonstrates that the resource is not an adequate substitute, implications regarding welfare should be drawn cautiously.

Behavior may also be dysfunctional due to a lack of "fit" between the captive environment and the animal's evolved behavior. Research or farm environments provide a range of supernormal and subnormal stimuli, relative to those found in the evolutionary environment; so the animal may be subject to a lack of environmental stimulation leading to boredom, redirection of motivated behavior, or an inability to perceive its environment fully and thus interact with it. For example, the vision of chickens and turkeys is skewed, relative to human vision, toward the UV spectrum. However, lighting in many commercial farm housing units omits UV wavelengths, which has the potential for affecting the animals'

ability to perceive resources such as food and water or perceive and discriminate between conspecifics (e.g., Manser 1996; Prescott and Wathes 1999), even though turkeys have been shown to prefer environments that are illuminated with UV spectrum light (Moinard and Sherwin 1999). Apparently benign stimuli, such as a human entering a home pen or the presence of a red-colored object, may elicit fear and cause escape behavior if these stimulus properties cued dangerous situations in the evolutionary environment (Dawkins 1999).

Social interactions in industrial-scale commercial agricultural production can also vary notably from those found in the evolutionary environment. This variation may have both positive and negative implications for psychological and physical welfare. For example, laying hens reared in large flocks show reduced levels of aggression compared with those in small colonies (Hughes et al. 1997), although the frequency and prevalence of aggressive interactions and mortal injury are particularly high in broiler breeder strain chickens (King 2001a; Millman and Duncan 2000). Like aggression, social facilitation may be a normal aspect of evolved behavior; however, it may also have implications for welfare, for example, through the transmission of injurious behaviors such as feather-pecking between flock members, which can rapidly decimate flocks of loose-housed laying hens (e.g., Green et al. 2000; Nicol 1995). The frequency and prevalence of aggression, aversive or fear-inducing stimuli, or avoidance behavior may provide indications of the extent of adversity encountered by animals in particular research or production environments. Cognitive studies such as object-discrimination research and ethological field-based studies of wild ancestors and feral conspecifics can provide predictive indications of potential stimuli that have implications for welfare, for example, suggesting resources that may be important to include in the captive environment, or demonstrating social behaviors that may influence fear in agricultural animals (Mayer et al. 2002; McBride et al. 1969; Savory et al. 1978).

Stereotypies

One category of behavior that has drawn much attention in terms of animal welfare is that of stereotypies, or repetitive, invariant, nonfunctional behaviors (Dantzer 1991; Mason 1991a,b). Stereotypies may indicate that an animal is unable to perform motivated functional behavior when interacting with its current environment and may consequently experience unpleasant subjective states associated with frustration (Duncan and Wood-Gush 1972; Mason 1991a,b). Stereotypies are ethologically abnormal in several senses: (1) Stereotypies are not functionally appropriate in the context of available environmental stimuli; (2) patterns of behavioral sequencing may be unusual in comparison with animals reared in complex environments or observed in the evolutionary environment; (3) they do not occur in animals observed in the "wild" or may occupy unusual proportions of the time available for performance of behavior (Mason 1991a,b).

Stereotypies may also be abnormal in the sense that they lead to injury, or that they occur instead of functional behavior appropriate to the environmental stimuli present (Duncan and Wood-Gush 1972; Mason 1991a). Stereotypies may indicate that welfare is compromised inasmuch as the current environment does not contain resources with which the animal is intrinsically motivated to interact; however, this is not always the case because stereotypies may also appear as "behavioral scars" arising from prior experience of impoverished environments (Mason 1991a,b). Some stereotypies may be difficult to differentiate from behavior patterns that are naturally stereotyped in form, such as pacing or pecking (e.g., Kostal et al. 1992), although close observation of sequential patterning or the location where the behavior occurs in the home environment may indicate reduced variance (King 2002). Behavior performed toward nonfunctional objects may indeed be a functional response from the animal's perspective in that the qualities of visual stimuli or texture of an object in a captive environment may be perceived by the animal as being a stimulus for a particular behavior and therefore a suitable substitute

resource for the behavior (Dawkins 1998). The morphology and timing of stereotypies may also reflect evolutionary differences in species-specific control of behavior (e.g., the control of feeding or foraging behavior) but not necessarily indicate a welfare problem (Mason and Mendl 1997). However, there is evidence of correlation between the extent of stereotypy and frustrated motivation in some species (Savory et al. 1993).

Stereotypies may also occur only temporarily and be modifiable with simple environmental enrichment, such as nesting material or foraging resources (King 2001a; Wurbel 2001). The success of enrichment may depend on the extent to which the stereotypic behavior has become established (Cooper et al. 1996; Wurbel 2001).

Stereotypies are heterogeneous, therefore knowledge of the ontogeny of stereotypy is valuable to explain the behavior that is being observed, its consequences for research data and psychological welfare, and practical solutions for its improvement (Mason 1991a,b). The originating behavior may be indicated by the form that the stereotypy takes. For example, feed-deprived hens that are subsequently thwarted from accessing feed have been shown to attempt initially to escape their cage but to develop later similar pacing behavior around the cage perimeter and no longer respond to functional escape cues, such as the opening of the cage door (Duncan and Wood-Gush 1972). Some authors have suggested that stereotypies are a coping mechanism in impoverished environments or in response to poor psychological welfare, or may alternatively be rewarding (Broom 1991; Savory et al. 1992; Zanella et al. 1996; discussed further in Mason 1991a,b); however, other evidence suggests that this is not necessarily the case (e.g., Dantzer 1991; Wurbel and Stauffacher 1996; Wurbel et al. 1998).

Even with the foregoing list of qualifications, the performance of stereotypy should provide a red flag and warrant further investigation regarding potential behavioral and/or psychological deprivation in laboratory and agricultural environments (Appleby and Lawrence 1987; Mason and Mendl 1993). Indeed, recent evidence has suggested that in some cases, stereotypic behavior may reflect an underlying psychiatric dysfunction, indicating changes in neurophysiology that lead to an inability to perform flexible behavior (Garner and Mason 2002; Garner et al. 2001, 2003). If this is the case, preventing the development of stereotypy becomes important for reasons other than animal welfare. Stereotyping animals have the potential for providing skewed results in any research that requires flexible responses, such as open field tests or radial arm maze tests in which behavioral indications of cognitive function are used or in which behavioral or physiological measures are influenced by the extent of locomotory or other activity. Furthermore, because the extent of stereotypy within a group of animals often shows notable individual variation, stereotypy within a group of experimental subjects may increase uncontrolled variation and therefore "noise" in data arising from tests relying on flexibility of response (Garner 2002; Wurbel 2000).

Environmental Modifications and Animal Welfare

Captive environments are often characterized by a reduced complexity of resources, which may contain both supernormal and subnormal stimuli relative to the evolutionary environment (Dawkins 1999; Manser 1996; Wemelsfelder 1993, 1997). Environmental enrichment of captive housing involves altering the provision of social, physical, or sensory stimuli in the environment so as to improve physical health or psychological welfare. Enrichment can take many forms, such as the number, density, sex, appearance, and familiarity of conspecifics, which may alter the quality and type of conspecifics social interactions; the presence, predictability, appearance, and quality of interaction with humans; the patterning of sensory stimuli such as light schedules, UV spectra, or "patchiness" of light distribution in the pen; and the provision of complex or novel stimuli or those resources with which the animal is motivated to interact, as discussed above. Environmental modifications may directly alter behavior, cognition, and/or welfare by

providing resources that allow animals to perform specific behaviors (e.g., jumping, resting undisturbed, nest-building). However, these changes may also alter welfare through the provision of increased complexity (e.g., leading to greater exploratory behavior [Mench 1998]) or alter social interactions by changing the spatial distribution of groups of animals, or the behavior or orientation of an animal when it is encountered by other flockmates (e.g., Kells et al. 2001; King 2001a).

Enrichments that are based on the wide and developing scientific knowledge of agricultural animals' behavioral requirements may be highly beneficial for research animals housed on farms and in laboratories. Evidence from consumer demand and preference studies, along with knowledge of the physical and social aspects of the evolutionary environment, can indicate what kind of resources may be most likely to improve welfare (Newberry 1995). It is important to differentiate environmental enrichment that affects the animal's physical or psychological state positively from environmental modifications that simply alter behavior (Duncan and Olsson 2001; Olsson and Dahlborn 2002).

Environmental enrichments can have many effects on welfare, such as altering locomotory behavior and having potential consequences for physical health and development (Newman and Leeson 1998), as well as altering enclosure use, social interactions, and potentially injurious behaviors such as aggression (Cornetto and Estevez 2001; Kells et al. 2001; King 2001a; O'Connell and Beattie 1999). Providing resources that the animal is motivated to obtain may alter its underlying psychological state by reducing frustration or increasing positive emotional responses, as discussed above.

Sometimes the provision of specific resources is necessary for environmental enrichment to affect welfare, or, alternatively, enrichment may be necessary at certain "sensitive" periods in development to influence behavior or cognition (e.g., providing perches for hens [Gunnarsson et al. 2000]). Increasing complexity may facilitate exploration and increase cognitive capacity, or it may alter cognitive capabilities such as spatial problem-solving (de Jong et al. 2000; Gunnarsson et al. 2000). Environmental modifications may also alter physiological responses (de Jong et al. 2000), brain structure, and gene expression (Rampon et al. 2000), or they may alter disease progression (Hockly et al. 2002). These issues are particularly important in experimental conditions that aim to reduce uncontrolled variation. Recent evidence suggests that standardization of captive housing using environments that have a minimal complexity of environmental stimuli may increase, rather than reduce, individual variation in test performance or behavior (Garner 2002; Garner and Mason 2002; Kostal et al. 1992).

Information Sources for Environmental Enrichment

There is a wealth of information available on behavioral, environmental, and resource requirements, particularly for agricultural animals, which have been a primary focus of scientific animal welfare research. Sources include (but are not limited to) the following:

- Databases such as the Animal Welfare Information Center (AWIC1) (<http://www.nal.usda.gov/awic/pubs/enrich/intro.htm>); and the Animal Welfare Institute (AWI1) (http://www.awionline.org/lab_animals/newindex.html)
- Publications such as Comfortable Quarters (produced by AWI)
- Guidance documents and books from the Federation of Animal Science Societies (FASS 1999), the Universities Federation for Animal Welfare (UFAW1), and Scientists Center for Animal Welfare (SCAW1)

- Peer-reviewed scientific journals such as Applied Animal Behaviour Science, Animal Welfare, and the Journal of Applied Animal Welfare Science

Other publications feature animal welfare-related research articles such as Behavioural Processes and Animal Behaviour. Agricultural production journals such as the Journal of Animal Science and World's Poultry Science Journal also carry welfare science articles. The UK government's advisory panel, the Farm Animal Welfare Council (<http://www.fawc.org.uk/>), also produces a range of review documents relating to the welfare of particular agricultural species and commercially used animal strains. Together, these resources provide extensive information on species-specific resource requirements and practical, convenient, inexpensive enrichments for agricultural animals. Furthermore, many scientific journal search engines such as PubMed (<http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=journals>) and Web of Science (<http://wos.mimas.ac.uk>) carry journals that cover animal welfare and environmental enrichment topics. Altweb (<http://altweb.jhsph.edu/>) provides a valuable gateway for information on the 3Rs, including environmental enrichment.

Applied Animal Welfare: Implications for Experimental Design

There is a range of applied issues associated with the psychological welfare of agricultural production animals in research. Some examples of solutions are discussed below, with a focus on the practical application of the 3Rs to animal use that may lead to distress or suffering (Russell and Burch 1959).

Commercial agricultural environments are primarily designed for production efficiency, so these conditions may not meet species' behavioral and psychological requirements (Dawkins 1980, 1999). Genetic strains of particular species used in certain types of agricultural production are strongly selected for particular traits, and such strains may be prone to particular welfare problems. For example, broiler meat chickens have been strongly selected for growth traits because they reach a finishing weight of 2.4 to 3.2 kg in only 42 to 49 days (www.rossbreeders.com, accessed 10/22/02). This rapid rate of growth is associated with lameness and respiratory disorders (Zubair and Leeson 1996). The growth rates in broiler breeders and pigs require management through restriction of feed intake, which leads to frustration of feeding motivation and a potentially unpleasant subjective state associated with hunger (e.g., Hocking 1993; Hocking et al. 1993). Some genetic strains of agricultural animals may be particularly aggressive (e.g., Millman and Duncan 2000) and may injure conspecifics (King 2001a). In these cases, there may be ethical issues related to creation of experimental populations that may inevitably experience distress, physical suffering, or mortality.

One alternative for agricultural production or animal welfare research is to use pre-existing populations through partnerships with industrial agricultural producers (i.e., sample populations housed in commercial conditions). Farm-based studies can have good external validity, although careful consideration is required regarding potential confounding variables, uncontrolled variation, and limitations on the extent of replication and statistical requirements for experimental design (Hall 2001; Kells et al. 2001; King 2001a).

There are many ways in which the likelihood of animal distress or suffering can be reduced when performing research on agricultural animals by practically employing the 3Rs in experimental design (Russell and Burch 1959). The negative impact of research on physiological and psychological welfare can be reduced through addressing both the number of animals used and the extent of individual distress. With advice from a biostatistician regarding experimental design, it is possible to identify the appropriate sample size for a particular study, make maximal use of small sample sizes, and increase research

efficiency by reducing the requirements for replication. Recently published dedicated guidance is available for the design of animal experiments (Festing 2002; Festing et al. 2002).

The use of noninvasive measures can reduce pain and distress associated with procedures such as blood sampling. In test environments, these measures can also reduce the influence of physiological and behavioral responses that are the result of fear and stress associated with handling. Among the new techniques that have recently been validated is the noninvasive measurement of fecal corticosteroids (Lord 2003).

As discussed above, it is important to identify and make use of the environmental requirements of agricultural species (Granstrom 2003). If that is not possible, there must be justification for the selection of the environment (e.g., to mimic an actual production environment). It is also important to consult the scientific literature to identify species- or strain-typical behavioral and resource requirements, particularly when using a new species or genetic strain.

The development of simple, practical welfare auditing processes is a useful means of monitoring the long-term well-being of research populations. It may also be beneficial in indicating potential confounds or uncontrolled variation within the research study that are associated with poor health or distress. Accordingly, animals should also be monitored periodically for the development of abnormal behaviors, which may indicate that environmental requirements have not been met.

Distress may occur as a direct or an indirect aspect of the study, particularly in animal welfare research. Distress associated with pain can be minimized by testing animals using methods that evaluate behavior during analgesia, rather than when they are experiencing unmediated pain (e.g., Danbury et al. 2000). Considerations should be made of the cognitive and locomotory effects of analgesics, however, to prevent potentially confounding responses. When aggression is a factor in the study, clear thresholds for the extent of aggression or associated mortality should be identified before the research commences. Where exposure to aggressive or aversive social interaction is a critical element of the research, minimization of exposure through experimental design should be a priority (D'Eath and Pickup 2002; Millman and Duncan 2000).

Exposure to potentially distressing stimuli should be minimized in both housing and experimental design. For example, when reinforcement schedules are used, positive rewards, rather than negative stimuli, should be employed when possible, and deprivation periods should be minimized. It is also worthwhile to consider the stock person's or technician's behavior toward experimental subjects in that positive human-animal interactions have been shown to alter behavior and reduce aversion in agricultural animals. Such interactions have also been shown to influence production outcomes in pigs, dairy cows, and, more equivocally, in broiler chickens (Cransberg et al. 2000; Hemsworth et al. 2000, 2002). The potential for human-animal interactions to cause fear or distress can be minimized by using remote technologies such as video and telemetry for behavioral and physiological recording (e.g., Cook et al. 2000; Hall 2001).

Good practice requires the critical evaluation of all research for potential costs and benefits. Indeed, regulatory requirements of US Public Health Service-funded research using agricultural animals for biomedical and nonagricultural purposes specifically include consideration of animal welfare and alternatives, including housing, husbandry, and environmental enrichment (NRC 1996) (<http://www.aphis.usda.gov/ac/policy/policy29.pdf>). Furthermore, ethical and methodological deliberations can be included in the experimental design section of journal reports to promulgate this best practice. In this way, the important work of the scientific community in recognizing and addressing the welfare of research animals will be clearly demonstrated to scientists, regulators, and the public.

Summary and Conclusions

The prevailing public ethic increasingly emphasizes a responsibility for animal welfare when animals are used by humans for food production or research (Rollin 1995). Although much attention has been given to indicators of animal health, psychological welfare is also an important consideration for animals that are capable of experiencing emotional states. Scientific, operational measurements of behavior and performance in psychological tests can provide objective, quantifiable correlates of the psychological welfare of agricultural animals while also identifying animals' environmental and husbandry requirements.

Consumer demand is one, but not the only, tool for measuring animal welfare, and neither should it be. After all, animals do not come with ready-made welfare indicators. Rather, their behavior and physiology reflect coordinated responses to environmental challenges, which may be diverse in form and dependent on both cognitions and subjective state (Dawkins 1999; Mason and Mendl 1993). These measures of motivated behavior coupled with physiological data may provide a useful indicator of animal choices and priorities, as well as an overall picture of the effects of husbandry, handling, and experimental procedures, while other behaviors may reflect an animal's inability to interact functionally with the environment and provide a red flag to potential causes of distress. As knowledge of the ontogeny of abnormal behavior and psychological functioning develops further, we will have a better understanding of how our use of animals, whether on the farm or in the laboratory, affects both their psychological and physical welfare.

Whether on the research farm or inside the laboratory, simple changes in terms of enrichment, information searches, and consideration of welfare in experimental design can reap rewards both for scientific knowledge and for animal welfare (King 2001b). Professional scientific advice on psychological welfare is available in a range of media sources and from dedicated organizations such as AWIC, UFAW, and SCAW. The scientific community has come a long way in a short time toward understanding and incorporating knowledge of agricultural animal welfare in experimental design, housing, and husbandry. On this basis, best practice should be recorded to demonstrate this progress to peers and the public. Simple, straightforward solutions are available to minimize distress in experimental agricultural animals, to optimize good welfare, and to ensure that animal welfare and good science go hand in hand.

Acknowledgments

This manuscript was developed with the support of a UK Ministry of Agriculture (DEFRA) CASE studentship held at the Department of Zoology, University of Oxford, UK. The author acknowledges the invaluable advice of Professor Marian Dawkins in the development of the manuscript.

Footnotes

¹Abbreviations used in this article: 3Rs, refinement, reduction, and replacement of animals in research; AWI, Animal Welfare Institute; AWIC, Animal Welfare Information Center; SCAW, Scientists Center for Animal Welfare; UFAW, Universities Federation for Animal Welfare; UV, ultraviolet.

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