ELSEVIER

Applied Animal Behaviour Science 44 (1995) 229–243

APPLIED ANIMAL BEHAVIOUR SCIENCE

# Environmental enrichment: Increasing the biological relevance of captive environments

Ruth C. Newberry

*Pacific Agriculture Research Centre (Agassiz), P.O. Box 1000, Agassiz, B.C. V0M 1A0, Canada*

**Abstract**

Environmental enrichment is a vague concept referring to improvements to captive animal environments. Some authors have applied the term to an environmental treatment itself, without any concrete evidence that the treatment represented an improvement for the animals. Others have used the term when the main beneficiaries may have been people rather than their captive animals. The criteria used to assess enrichment have also varied according to animal use (e.g. laboratory, farm or zoo animals). In this paper, environmental enrichment is defined as an improvement in the biological functioning of captive animals resulting from modifications to their environment. Evidence of improved biological functioning could include increased lifetime reproductive success, increased inclusive fitness or a correlate of these such as improved health. However, specifying an appropriate endpoint is problematic, especially for domestic animals. Potential methods of achieving enrichment that require further investigation include presenting food in ways that stimulate foraging behaviour and dividing enclosures into different functional areas. The quality of the external environment within the animals' sensory range also deserves greater attention. A common shortcoming of attempts at environmental enrichment is the provision of toys, music or other stimuli having little functional relevance to the animals. Failure to consider the effects of developmental factors and previous experience can also produce poor results. Environmental enrichment is constrained by financial costs and time demands on caretakers, and providing live prey to enrich the environment of predators raises ethical concerns. Future research on environmental enrichment would benefit from improved knowledge of the functions of behaviour performed in captivity and more rigorous experimental design.

*Keywords:* Environmental enrichment; Review; Natural behaviour; Animal welfare

## 1. Environmental enrichment—what is it?

Environmental enrichment is a popular goal of research in the field of applied ethology. However, like the concepts of "animal welfare" and "stress", it is a vague notion that

Elsevier Science B.V.
*SSDI* 0168-1591(95)00616-8

evades precise definition and is used inconsistently in the literature. In different studies, the initial (control) environment varies from wire cages containing single animals to large enclosures containing many animals. Methods used to attain enrichment range from adding a single object or material to the existing environment, such as a ball or some straw, to making a major change in the housing environment, such as placing animals in a semi-natural outdoor enclosure. The results obtained from these modifications represent changes in magnitude compared to the control treatment rather than attainment of a precise biological endpoint. There are no standardised methods or criteria for assessing whether enrichment has occurred.

The term "enrichment" implies an improvement. However, the term is frequently applied to types of environmental change (e.g. social, physical, sensory, feeding, taming) rather than the outcome, and some authors use enrichment as a synonym for an increase in complexity. Experimental treatments may be labelled barren versus enriched, before any evidence of an enriching effect has been presented. Usually, enrichment refers to a benefit for the animals. However, some authors use the term to refer to benefits to the owners or caretakers of the animals rather than the animals themselves.

In this paper, I define environmental enrichment as an improvement in the biological functioning of captive animals resulting from modifications to their environment. Evidence of improved biological functioning could include increased lifetime reproductive success, increased inclusive fitness (see Grafen, 1991), or a correlate of these such as improved health. However, specifying appropriate and practical measures of enrichment is problematic, especially for non-breeding domestic animals.

## 2. Theoretical basis for environmental enrichment research

Lack of an explicit theoretical framework for environmental enrichment is a current problem in applied ethology. Research objectives are often vague, the choice of assessment parameters perplexing, and the results difficult to interpret. If progress is to be made, a theoretical framework must be presented, from which specific hypotheses, predictions and assumptions are derived and tested. Promoting natural behaviour, and improving animal welfare, are two commonly stated, overlapping goals of environmental enrichment research. In this section, I discuss problems with these criteria as measures of enrichment.

### *2.1. Promoting natural behaviour*

Many authors advocate providing an environment which promotes natural behaviour (e.g. Pereira et al., 1989; Moodie and Chamove, 1990; Gilloux et al., 1992). However, because there is no single standard for natural behaviour or a natural environment, it is often unclear what is meant by natural behaviour. Is it the behaviour of captive animals when given more space or allowed outdoors? Is it behaviour adapted to the habitat from which the animals or their predecessors were caught? Does it refer to a wide range of behaviour exhibited by wild or feral populations of the same species living in a variety of habitats? If the objective is environmental enrichment, it is necessary to describe the desired behaviour and explain how the animals will benefit from exhibiting that behaviour.

For animals in genetic conservation programmes, enrichment should result from modifications to make the captive environment more similar to the environment where the animals are destined to be released. Future survival and reproductive success should be enhanced by providing opportunities to learn the characteristics of natural food items and predators at appropriate stages of development and to develop behavioural flexibility in response to a dynamic environment (Snowdon and Savage, 1989; Miller et al., 1990; Shepherdson, 1994).

Modifying the environment to resemble the future release site may also facilitate efforts to breed endangered species in captivity for future reintroduction, especially if the release site is the same as, or similar to, the capture site. By this method, there may be less risk of omitting important structural, climatic, social or nutritional features from the captive environment due to our lack of knowledge of the animals' specific requirements. On the other hand, it should be recognised that captive environments are typically characterised by high population densities, limited space, low predation pressure, readily available food, and physical barriers preventing dispersal and immigration (Newberry, 1993). Over generations, the genetic structure of populations exposed to these conditions will shift in favour of more sedentary behaviour and reduced wariness, as the population adapts to captivity. Because such behaviour would be maladaptive in most wild habitats, and because such selection forces are difficult to avoid in captivity, emphasis should probably be placed on preserving wild habitats and minimising time in captivity rather than relying on enrichment techniques to allow long-term maintenance in captivity.

By contrast with populations destined for release, it is neither necessary nor desirable for animals that are kept indefinitely in captivity for use by people to remain adapted to natural environments. Their success in captivity will depend upon their ability to adapt to captive conditions. Furthermore, domestic animals are subjected to artificial selection to enhance traits desired by humans, and animals such as dairy cattle and domestic turkeys are not required to breed naturally or rear their own young. It is true that even highly domesticated animals retain a behavioural repertoire shaped by natural selection during their evolutionary history, and exhibit this behaviour to varying degrees when kept in semi-natural environments (e.g. Newberry and Wood-Gush, 1988; Stolba and Wood-Gush, 1989; Love, 1994). However, because their behaviour has also been influenced by both natural and artificial selection in captivity, it is difficult to specify an appropriate model for their "natural" behaviour. To what extent should their behaviour resemble that performed in more extensive or natural environments? For example, should we encourage these animals to perform more anti-predator behaviour through exposure to predator models, as done by Moodie and Chamove (1990)? Should we require these animals to spend more time foraging so that their behavioural time budget more closely resembles that of wild populations (McFarland, 1989)?

In general, I suggest that it is more useful to emphasise the functionality and adaptiveness of behaviour in specific environments than its "naturalness". For this purpose, we should attempt to determine how well individuals and populations are able to adapt to a range of different captive environments. Studies of adaptation tend to emphasise physiological mechanisms. However, it is equally important that we improve our knowledge of behavioural plasticity and rules underlying behavioural decisions in captive environments.

### 2.3. Improving animal welfare

Abnormal behaviour is often taken as an indicator of reduced welfare, prompting research to enrich the environment through modifications that reduce abnormal behaviour (e.g. Kastelein and Wiepkema, 1989; Bayne et al., 1992). However, the relationship between abnormal behaviour such as stereotypies and welfare is uncertain (Mason, 1991). Some behaviour currently considered abnormal may in fact be adaptive in captivity, conferring a selective advantage on individuals performing the behaviour. Instead of jumping to the conclusion that certain forms of behaviour shown in captivity are bad for welfare and that enrichment will result if the animals stop performing them, I suggest that our first step should be to quantify the costs and benefits to the individual of performing the behaviour.

Enrichment attempts are also aimed at reducing negative emotional states. These include fear and stress associated with exposure to novel stimuli (Grandin, 1989; Nicol, 1992; Jones and Waddington, 1992; Pearce and Paterson, 1993), boredom and apathy postulated to result from housing in unstimulating environments (Wood-Gush and Vestergaard, 1989; Wemelsfelder, 1991), and frustration which animals may experience when unable to express behaviour that they are motivated to perform (Duncan, 1970; Gilloux et al., 1992). It has been argued that animals will suffer if unable to perform the behaviour even if it is not necessary to meet immediate physiological requirements (Hughes and Duncan, 1988; Jensen and Toates, 1993). Furthermore, because survival in the wild requires successful execution of goal-directed behaviour, it has been suggested on evolutionary grounds that performing this behaviour is rewarding (Dawkins, 1990; Shepherdson et al., 1989b). The difficulty with this approach to environmental enrichment is that emotional states cannot (yet) be measured directly. Therefore, it is not possible to obtain concrete evidence that an environmental change has resulted in enrichment by replacing negative with positive emotional states.

Environmental modifications have also been aimed at improving welfare by improving physical health. Methods have included occupying animals in harmless activities instead of biting, chewing and pecking at pen mates (Feddes and Fraser, 1993; Nørgaard-Nielsen et al., 1993; Gvaryahu et al., 1994), providing opportunities to avoid harmful aggression (Erwin et al., 1976), reducing escape responses during handling to decrease the risk of injury (Reed et al., 1993), and promoting a wide range of movement to improve muscular, skeletal and cardiovascular fitness (Chamove, 1989; King and Norwood, 1989). I suggest that promoting physical health is a realistic objective of enrichment attempts because benefits to the animals can be measured directly and because good health should be a prerequisite for high reproductive success and inclusive fitness.

## 3. Animal use affects environmental enrichment research

Confusion in the environmental enrichment literature is heightened by differences in emphasis depending upon the purpose for keeping the animals. For laboratory animals, enrichment research has been prompted by concerns about the validity and applicability of research results obtained from subjects housed in standard laboratory cages (e.g. Gentile and Beheshti, 1987; O'Neill, 1989; Carughi et al., 1989; Bayne et al., 1992; Widman et al., 1992). For farm animals, enrichment studies have emphasised methods to improve the public image of animal production (Curtis, 1993), or to increase economic returns by boosting growth rate, feed conversion efficiency or egg production (e.g. Gvaryahu et al., 1989; Church et al., 1993; Curtis, 1993). For zoo animals, consideration has been given to the "holding power" of exhibits, which is improved if animals are busily engaged in naturalistic behaviour rather than resting, hiding out of sight, or performing behaviour considered abnormal, unpleasant or disgusting by the public (Akers and Schildkraut, 1985; Shepherdson et al., 1989b, 1993).

Thus, in some cases the underlying motive for so-called environmental enrichment research may be to enhance the utility of the animals to their owners (i.e. to "enrich" people). Although all research is influenced by economic costs and benefits, it would be misleading to invoke environmental enrichment as the primary goal of the research if the main emphasis is on benefits to people.

## 4. Methods of achieving environmental enrichment

A variety of methods have been used in attempts at environmental enrichment. Rather than presenting a comprehensive review, I shall focus on three promising topics for enrichment research—altering feeding methods, dividing the environment into different functional areas, and creating a more appropriate external environment.

### *4.1. Feeding methods*

Captive animals are usually provided with a more limited selection of food types than those available in natural habitats. Offering a wider selection of food types is a potential source of enrichment, especially for species with generalist diets. Greater food variety could stimulate food searching and handling behaviour, thereby improving physical condition. Increased choice of food items could also improve nutritional balance (Pereira et al., 1989), especially when nutrient requirements are changing due to temperature fluctuations and developmental changes (Scott and Balnave, 1988).

Food intake in captivity often requires different behaviour than that performed when feeding in the wild. However, animals may still attempt to perform the components of feeding behaviour that have been shaped by natural selection during their evolutionary history. In the absence of an appropriate substrate, this behaviour may be directed towards pen mates or pen fixtures with harmful effects (Fraser, 1989). This problem can be solved by identifying and providing appropriate substrates. Thus, concern about injuries and other health risks caused by cross-sucking in group-housed veal calves led to the discovery that cross-sucking could be reduced by providing each calf with a dummy teat to suck after bucket feeding (A.M.B. de Passillé, personal communication, 1994). Sucking a dummy teat also elevated the levels of insulin and other digestive hormones in the blood of singly-housed calves (de Passillé et al., 1993). The results support the idea that behaviour that may initially appear to be a functionless artifact (e.g. cross-sucking) may actually provide functional benefits to the performer. By providing a dummy teat, enrichment should result in reduced injuries to the recipients of cross-sucking. The performer may also benefit from improved health if the dummy teat provides a more effective sucking substrate than another calf.

Providing earth or straw as a foraging substrate has met with varied success. Rooting by pigs in a trough filled with earth diminished over time and was not linked in functional sequences with other feeding activities (Appleby and Wood-Gush, 1988). However, Fraser et al. (1991) obtained good results with straw, which was renewed daily. The novelty of the straw, and its greater palatability, could have contributed to this difference. An inedible substrate may not sustain prolonged levels of investigation if it is not renewed and if the foraging behaviour never results in a functional consequence, such as the occasional discovery of food.

Whereas in natural habitats foraging usually constitutes a major portion of the behavioural time budget, in captivity food is dispensed in highly predictable locations in an easily consumed form, resulting in minimal searching and handling times (Newberry, 1993). Moreover, food may only be provided once or twice a day in limited quantities. These feeding conditions contribute to the development of certain forms of stereotyped behaviour in captivity (Rushen, 1984; Terlouw et al., 1991). These stereotypies can be reduced by providing more of the same food (Terlouw et al., 1991; Lawrence and Terlouw, 1993) but this contributes to obesity, resulting in health and reproductive problems. However, there may also be reproductive costs to animals from performing stereotyped behaviour (Von Borell and Hurnik, 1990).

Much enrichment research has been directed towards feeding methods aimed at reducing food-related stereotypies. Methods have included providing smaller, more frequent meals, scattering and hiding food in unpredictable locations, increasing the time and skill required to catch or extract food (e.g. by providing live prey), increasing the time required to process and ingest food, and increasing dietary fibre content to promote satiety (Chamove et al., 1982; Kastelein and Wiepkema, 1989; King and Norwood, 1989; Shepherdson et al., 1989b; Carlstead et al., 1991; Gilloux et al., 1992; Shepherdson et al., 1993; Robert et al., 1993; Reinhardt, 1994; Brouns et al., 1994; Young et al., 1994). The relative merits of these different feeding techniques are unclear because, in different studies, they have been applied in combination, confounded with nutritional content, tested on only one or a few animals, applied sequentially for short periods with possible confounding by residual effects of previous treatments, and assessed by different measures. The effects of feeding habits and learning ability of individuals at different ages, and the influence of social dynamics on access to food, also need to be taken into account (Chamove et al., 1982; Anderson et al., 1994). Rather than restricting attention to stereotyped behaviour, I recommend that systematic research be undertaken to evaluate the relative merits of these feeding methods on health, reproductive success and inclusive fitness.

### 4.2. *The physical structure of the environment*

Animal housing is often characterised by flat, featureless walls and floors, and an absence of internal structure. Environmental complexity can be increased by adding an upper tier or vertical partitions to divide the space into different functional areas (Fraser et al., 1986; Simonsen, 1990), and by adding biologically relevant features such as perches and dust bathing sites for chickens (Newberry, 1993). Walls may be made more inhabitable for some species by providing ledges and climbing holds, and a feeling of security may be enhanced by providing opportunities for camouflage and hiding. Access to alternate enclosures indoors or outdoors can provide increased opportunities for exploration, patrolling and choice of social companions (Rumbaugh et al., 1989; Newberry, 1993). Providing opportunities for exploration could be especially useful to animals adapted to unpredictable environments (Mench, 1995). We need more information about net benefits to animals from making these types of modification to assess their enrichment value.

### *4.3. The external environment—what's beyond the four walls?*

Consideration should be directed not only to the internal environment of the enclosure but also to the surrounding area within the animals' sensory range. For some species, the view of the external environment may affect health. For example, human patients recovered more rapidly from surgery in rooms with an outdoor view of trees than an outlook on a brick wall (Ulrich, 1984). Other species may also benefit from a room with a view. We know that dogs and silver foxes use a raised platform in their cage as a look-out if it affords a view of neighbouring animals and the approach of people (Hubrecht, 1993; Mononen et al., 1993) and there is a report that singly-housed monkeys showed less abnormal behaviour when located in a cage next to a window (O'Neill, 1989). Televised images may have some value in allowing animals to monitor events in the external surroundings if they can perceive the images on the screen and if the images provide them with useful information. Rumbaugh et al. (1989) reported that most chimpanzees can learn to perceive the relevance of images on a screen by watching real-world events on the screen and at the same time witnessing these events directly. They describe an occasion when chimpanzees were frightened by the sound of chain saws outdoors. Fear turned to fascination when they were able to observe the activities associated with the sound on closed-circuit television. On the other hand, Chamove et al. (1988) observed increased aggressiveness and stereotyped locomotion associated with the presence of visitors at primate zoo exhibits. These results led them to conclude that visitors were a source of stressful excitement rather than environmental enrichment. They recommended designing exhibits so that visitors appear smaller or less visible to the animals.

Greater attention to the sounds and odours coming from the external environment is also warranted. For example, Shepherdson et al. (1989a) broadcast the territorial song duet of a gibbon pair to a captive group, simulating the singing of a neighbouring group in the wild. The captive gibbons responded with their own duet. The researchers suggested that the auditory stimulus was a source of enrichment based on evidence that the gibbon duet is important for formation and maintenance of the pair bond, and that the opportunity to hear and respond to song duets can be used as a reward in an operant conditioning paradigm.

## 5. Toys and music—biologically relevant or anthropomorphic whims?

Enrichment attempts will fail if the environmental modifications have little functional significance to the animals, are not sufficiently focused to meet a specific goal, or are based on an incorrect hypothesis regarding the causation and mechanisms underlying a problem.

Efforts will also be hindered if animals are unable to control their exposure to social and physical stimuli. These problems are often encountered in research where enrichment has been sought through providing animals with toys or music.

### 5.1. Toys

Toys are often recommended as sources of environmental enrichment (e.g. Canadian Council on Animal Care, 1993). However, the term ''toys'' is a catch-all for many objects, such as rubber hoses, chains, cloth strips, car tyres, metal bars, dangling plastic objects, flavoured chews and food blocks (Grandin, 1989; Schaefer et al., 1990; Hubrecht, 1993; Pearce and Paterson, 1993; Gvaryahu et al., 1994). A collection of such items may be provided, either permanently or on a rotating basis, with animal responses being lumped together to indicate ''the effect of the toys''. However, some of the objects are likely to be of greater functional value to the animals than others, and there may be differences between group members in the value derived from specific objects. Furthermore, the term ''toys'' implies that the motivation underlying use of the objects is play. In reality, the motivational state underlying behaviour responses will vary according to the type of object and the ways in which it can be used.

It is perhaps not surprising that results obtained from providing toys are variable and open to different interpretations. Thus, Grandin (1989) reported that pigs provided with toys were more likely to approach people than pigs without toys, and interpreted this as evidence that the toys reduced fear. By contrast, Pearce and Paterson (1993) found that pigs reared with toys were slower to approach people than pigs reared without toys, which they interpreted as a sign that the pigs were less reactive to novelty. Gvaryahu et al. (1994) reported a reduction in aggression among laying hens when small plastic toys were hung in their cages. They interpreted the results as evidence that the objects reduced ''social pressure'' by redirecting aggression. However, F.E. Robinson (personal communication, 1994) interpreted higher rates of pecking at these devices by feed-restricted than full-fed chicks as evidence that feeding motivation, rather than aggression, underlay pecking at the devices.

There is a need for greater thought regarding the design of objects to achieve specific goals. For example, destructible items with nutritional value should be more relevant substrates for foraging behaviour than indestructible, inedible objects (Fraser, 1987; Feddes and Fraser, 1993). Appropriately designed refuges and feeding sites (Erwin et al., 1976; McGlone and Curtis, 1985; Simonsen, 1990) should be more effective in limiting aggression among group members than reliance on toys to distract animals from fighting. And novel objects which can be picked up and carried about are more likely to stimulate object play than heavy permanent fixtures (Newberry et al., 1988; Wood-Gush and Vestergaard, 1991).

The numbers and distribution of objects should also be considered. Limited numbers of valued objects or limited accessibility may provoke competition between group members and prevent subordinates from reaping any potential benefits from the objects (Hubrecht, 1993). And it should be remembered that just because animals investigate objects, or show some other change in behaviour in their presence, does not necessarily mean that they have an enriching effect. In a study with rhesus monkeys, Bayne et al. (1992) reported that one monkey, which had been performing high levels of repetitive picking at its cage, transferred a proportion of this behaviour to a set of objects added to the cage. Thus, ''toys'' should not be viewed as a panacea for achieving environmental enrichment. The term "toys" is anthropomorphic, and best avoided.

### 5.2. *Music, radio and other sounds*

Several studies have incorporated music recordings or radio broadcasts in environmental enrichment attempts. The value of this approach remains uncertain due to limited knowledge of bioacoustics in different species and difficulties in interpreting results of experiments with music or radio treatments. In some studies, music effects have been confounded with effects of other environmental variables (Gvaryahu et al., 1989; Nicol, 1992; Reed et al., 1993). In others, the measurements taken do not provide clear evidence of enrichment. For example, Ladd et al. (1992) reported that laying hens exposed to a country music radio station, or a classical/jazz station, did more head shaking and less preening than hens without a radio. "Country music" hens had longer feeding durations and lower heterophil:lymphocyte ratios than "classical/jazz" and "no radio" hens. Which aspects of the radio stations the hens were responding to is a mystery! In rhesus monkeys, more "affiliative" behaviour was shown when the monkeys were given a music box, but no significant effects on other behavioural measures or on cortisol levels were found (Novak and Drewson, 1989).

Even sounds of the natural habitat from which a captive population originated may have little meaning unless the animals have learned how to interpret the sounds. As with music and radio broadcasts, these sounds are complex and variable. Animal responses to a general recording of natural sounds will be difficult to interpret without prior knowledge of the characteristics of sounds having signal value to the animals, and the expected responses to those sounds (Guildford and Dawkins, 1991). Thus, Ogden et al. (1994) found no clear-cut benefit from playing a recording of tropical rain forest sounds to captive lowland gorillas. The adults responded with increased locomotion, which was interpreted as a negative effect indicating agitation. The infants responded with reduced clinging, which was interpreted as a positive sign that the sounds masked other noises.

Captive environments are often extremely noisy due to high stocking densities, forced-air ventilation, and use of non-porous building materials (e.g. Konovalov, 1986). Noisy environments can cause hearing impairment and upset communication between animals. For example, Algers and Jensen (1985, 1991) found that fan noise disrupted communication between sows and piglets during nursing, resulting in slower piglet growth. Adding auditory stimuli to an already noisy environment may do more harm than good, especially if the animals have no control over the sound, such as to the ability to move to a quieter location or to switch off the sound. Rhesus monkeys will switch music on and off frequently if given the opportunity (Markowitz and Line, 1989; Novak and Drewson, 1989).

## 6. Development, learning and previous experience

Learning occurring during ontogeny can have long-lasting effects on future behaviour, including preferences for food, mates, and habitat type. Thus, some environmental modifications will be less effective in enriching the environment if made after specific preferences and habits have developed (Mastika and Cumming, 1987; Cooper and Nicol, 1991). If chickens imprint on feathers as a dust bathing substrate in the absence of a more functional substrate (Nørgaard-Nielsen et al., 1993), they may continue to seek feathers for dust bathing even if subsequently supplied with a better substrate. Lack of opportunity to learn social and maternal skills when young can also result in maladaptive behaviour even though animals are later housed in a more appropriate social environment. Female rhesus monkeys separated from their mother after infancy, and unable to learn maternal skills by observing their mother interact with their younger siblings, may subsequently reject or neglect their own infants (Berman, 1990).

Animals transferred from a simple to a complex environment may have difficulty locating food and other resources (e.g. Steinruck et al., 1990). They require time to develop skills to negotiate their way through a complex, three dimensional space, such as correctly judging distances so they can land accurately after flying or leaping from one level to another. Adaptation to the new environment may be influenced by adverse effects of environmental conditions during rearing on brain development and spatial learning ability (Carughi et al., 1989; Widman et al., 1992). And allowance must be made for the animals' initial lack of physical strength and flexibility to move between different levels and around obstacles. These problems can be avoided by making environmental improvements before animals are born or when they are at a young age.

Because an enriched environment is beneficial to the animals, it follows that removal of enriching features, or transfer to an environment lacking these features, will have adverse effects. Bayne et al. (1992) noted that certain singly-housed rhesus monkeys showed higher levels of stereotyped behaviour after removal of enriching features than they had done in the period prior to adding these features. Nicol (1992) reported that chickens reared in pens containing a variety of objects, and habituated to gentle handling, showed stronger anti-predator responses following catching and transportation than chickens reared without these stimuli. She suggested that the chickens may have been more aware of the catching procedure due to enhanced perception, learning and memory abilities, or that catching and transportation may have destroyed a learnt expectancy that handling was "safe". Perhaps separation from aspects of the environment to which animals have become attached is more aversive than removal from an environment lacking these stimuli.

## 7. Constraints on environmental enrichment

Environmental enrichment is constrained by concerns about disease transmission associated with social housing, increased contact with excreta, and difficulty cleaning and disinfecting enclosures containing soil, logs and other porous materials. Because different environments favour different diseases, care must be taken that enrichment attempts result in a net benefit for the animals rather than merely substituting one problem for another. Nevertheless, some disease concerns have proved unfounded. Chamove et al. (1982) reported that spreading wood chip litter in monkey enclosures was more hygienic than having faeces and urine on bare concrete.

Methods used to achieve enrichment must be practical. Their adoption will be inhibited by problems obtaining specialised supplies, excessive cost of supplies and equipment, or excessive time demands upon staff. Thus, Shepherdson et al. (1989b) chose a simple, "low-tech" feed dispenser as an enrichment device over an electro-mechanical feed dispenser with microchip controller because it was less expensive and easier to maintain. Chamove (1989) noted that the time taken to bait tree stump feeders for tamarins was so great that the feeders would not be used by the staff despite some benefits. Analysis of advantages and disadvantages of different methods for both humans and captive animals can be useful in deciding which method to adopt (Chamove, 1989; Hubrecht, 1993; Love, 1994).

Human safety concerns provide another constraint on environmental enrichment, such as concerns about being bitten by loose-housed animals. Practical solutions must be developed to ensure human safety. For example, primate enclosures can be linked by tunnels constructed from holding cages, allowing animals to be caught easily when passing through a tunnel (J.A. Love, personal communication, 1994). Laboratory primates in relatively extensive housing conditions can be trained to present their tail through the enclosure rails for collection of blood samples (Pereira et al., 1989).

Ethical constraints surround the provision of live prey to predatory species. The behaviour of predators is altered by access to live prey. For example, squirrel monkeys used more time, effort, concentration and skill to catch live fish than to collect monkey chow from a bowl (King and Norwood, 1989). A fishing cat slept less, performed more diverse behaviour and used more of its enclosure after it was given live fish (Shepherdson et al., 1993). The predators may benefit from these behavioural changes although specific benefits need to be better identified. On the other hand, live prey clearly do not benefit from being caught by a predator, so there is some ethical concern even if the prey are low on the food chain, such as meal worms or crickets (Shepherdson et al., 1989b; Carlstead, 1991). A possible solution would be to design complex predator enclosures that can sustain a stable prey population. Alternatively, methods that stimulate beneficial behavioural changes without the use of live prey can be sought, such as hanging food high off the ground, putting it in deep water or moving it on a pulley system.

## 8. Conclusions

From this review of the literature, I suggest that the primary problem is the lack of a general theoretical framework for environmental enrichment. I have maintained that, for wild animals being held in captivity for future release, the captive environment should resemble the future release site as closely as possible. For animals being kept indefinitely in captivity, an appropriate model for an enriched environment is less clear. I have proposed that improved animal health, increased lifetime reproductive success or increased inclusive fitness resulting from environment modifications could constitute evidence of enrichment. However, I recognise the technical difficulties involved in assessing these parameters and encourage discussion on this topic. We need clearly defined and biologically meaningful goals for enrichment research if progress is to made in improving captive animal environments.

A secondary problem encountered in enrichment studies is a lack of rigorous scientific method. In many cases, solutions to behavioural problems are sought without an adequate understanding of the functional basis and motivation underlying behaviour performed in captive environments. This approach contributes to inefficient, trial and error research and incorrect interpretation of results. Furthermore, enrichment attempts often give the impression that they are based more on anthropomorphic feelings and on convenience than on biological relevance and functional utility to the animals. Enrichment research would be greatly improved by developing well-focused and well-founded hypotheses and predictions, and testing the hypotheses in a systematic manner with appropriate controls.

## Acknowledgements

I would like to thank A.M. de Passillé, D. Fraser, J. Love, F. Robinson, A. Schaefer, D. Shepherdson and A. Taylor for background material, and M. Appleby, L. De Pieri, I. Estevez, L. Fisher, L. Keeling, M. Knott and J. Rushen for constructive criticism of earlier versions of the manuscript.

## References

Akers, J.S. and Schildkraut, D.S., 1985. Regurgitation/reingestion and coprophagy in captive gorillas. Zoo Biol., 4: 99–109.

Algers, B. and Jensen, P., 1985. Communication during suckling in the domestic pig. Effects of continuous noise. Appl. Anim. Behav. Sci., 14: 49–61.

Algers, B. and Jensen, P., 1991. Teat stimulation and milk production in early lactation of sows. Effects of continuous noise. Can. J. Anim. Sci., 71: 51–60.

Anderson, J.R., Rortais, A. and Guillemein, S., 1994. Diving and swimming as enrichment activities for captive rhesus macaques (*Macaca mulatta*). Anim. Welfare, 3: 275–283.

Appleby, M.C. and Wood-Gush, D.G.M., 1988. Effect of earth as an additional stimulus on the behaviour of confined pigs. Behav. Proc., 17: 83–91.

Bayne, K.A.L., Hurst, J.K. and Dexter, S.L., 1992. Evaluation of the preference to and behavioral effects of an enriched environment on male rhesus monkeys. Lab. Anim. Sci., 42: 38–45.

Berman, C.M., 1990. Intergenerational transmission of maternal rejection rates among free-ranging rhesus monkeys. Anim. Behav., 39: 329–337.

Brouns, F., Edwards, S.A. and English, P.R., 1994. Effect of dietary fibre and feeding system on activity and oral behaviour of group housed sows. Appl. Anim. Behav. Sci., 39: 215–223.

Carlstead, K., 1991. Husbandry of the Fennec fox *Fennecus zerda*: environmental conditions influencing stereotypic behaviour. Int. Zoo Yearb., 30: 202–207.

Carlstead, K., Seidensticker, J. and Baldwin, R., 1991. Environmental enrichment for zoo bears. Zoo Biol., 10: 3–16.

Carughi, A., Carpenter, K.J. and Diamond, M.C., 1989. Effect of environmental enrichment during nutritional rehabilitation on body growth, blood parameters and cerebral cortical development of rats. J. Nutr., 119: 2005–2016.

Canadian Council on Animal Care, 1993. Guide to the Care and Use of Experimental Animals, Vol. 1, 2nd edn. E.D. Olfert, B.M. Cross and A.A. McWilliam (Editors), Canadian Council on Animal Care, Ottawa.

Chamove, A.S., 1989. Environmental enrichment: a review. Anim. Tech., 40: 155–178.

Chamove, A.S., Anderson, J.R., Morgan-Jones, S.C. and Jones, S., 1982. Deep woodchip litter: hygiene, feeding, and behavioral enhancement in eight primate species. Int. J. Stud. Anim. Prob., 3: 308–318.

Chamove, A.S., Hosey, G.R. and Schaetzel, P., 1988. Visitors excite primates in zoos. Zoo Biol., 7: 359–369.

Church, J.S., Tennessen, T. and Webster, A.B., 1993. Environmental enrichment influences the productivity and well-being of caged White-Leghorn hens. In: Proc. VII World Conf. Anim. Prod., Vol. 3. University of Alberta, Edmonton, pp. 369–370.

Cooper, J.J. and Nicol, C.J., 1991. Stereotypic behaviour affects environmental preference in bank voles, *Clethrionomys glareolus*. Anim. Behav., 41: 971–977.

Curtis, S.E., 1993. The physical environment and swine growth. In: G.R. Hollis (Editor), Growth of the Pig. CAB International, Wallingford, UK, pp. 93–105.

Dawkins, M.S., 1990. From an animal's point of view: motivation, fitness, and animal welfare. Behav. Brain Sci., 13: 1–61.

De Passillé, A.M.B., Christopherson, R. and Rushen, J., 1993. Non-nutritive sucking by the calf and postprandial secretion of insulin, CCK and gastrin. Physiol. Behav., 54: 1069–1073.

Duncan, I.J.H., 1970. Frustration in the fowl. In: B.M. Freeman and R.F. Gordon (Editors), Aspects of Poultry Behaviour. Br. Poult. Sci., Edinburgh, pp. 15–31.

Erwin, J., Anderson, B., Erwin, N., Lewis, L. and Flynn, D., 1976. Aggression in captive pigtail monkey groups: effects of provision of cover. Perceptual Motor Skill, 42: 319–324.

Feddes, J.J.R. and Fraser, D., 1993. Non-nutritive chewing by pigs: implications for tail-biting and behavioural enrichment. In: E. Collins and C. Boon (Editors), Livestock Environment IV. American Society of Agricultural Engineering, St. Joseph, MI, pp. 521–527.

Fraser, D., 1987. Mineral-deficient diets and the pig's attraction to blood: implications for tail biting. Can. J. Anim. Sci., 67: 909–918.

Fraser, D., 1989. Role of ethology in determining farm animal well-being. In: H.N. Guttman, J.A. Mench and R.C. Simmonds (Editors), Science and Animals: Addressing Contemporary Issues. Scientists Center for Animal Welfare, Bethesda, MD, pp. 95–102.

Fraser, D., Phillips, P.A. and Thompson, B.K., 1986. A test of a free-access two-level pen for fattening pigs. Anim. Prod., 42: 269–274.

Fraser, D., Phillips, P.A., Thompson, B.K. and Tennessen, T., 1991. Effect of straw on the behaviour of growing pigs. Appl. Anim. Behav. Sci., 30: 307–318.

Gentile, A.M. and Beheshti, Z., 1987. Enrichment versus exercise effects on motor impairments following cortical removals in rats. Behav. Neural Biol., 47: 321–332.

Gilloux, I., Gurnell, J. and Shepherdson, D., 1992. An enrichment device for great apes. Anim. Welfare, 1: 279–289.

Guildford, T. and Dawkins, M.S., 1991. Receiver psychology and the evolution of animal signals. Anim. Behav., 42: 1–14.

Grafen, A., 1991. Modelling in behavioural ecology. In: J.R. Krebs and N.B. Davies (Editors), Behavioural Ecology, 3rd edn. Blackwell, Oxford, UK, pp. 5–31.

Grandin, T., 1989. Environment and genetic effect on hog handling. Pap. No. 89-4514, American Society of Agricultural Engineering, St. Joseph, MI.

Gvaryahu, G., Cunningham, D.L. and van Tienhoven, A., 1989. Filial imprinting, environmental enrichment, and music application effects on behavior and performance of meat strain chicks. Poultry Sci., 68: 211–217.

Gvaryahu, G., Ararat, E., Asaf, E., Lev, M., Weller, J.I., Robinzon, B. and Snapir, N., 1994. An enrichment object that reduces aggressiveness and mortality in caged laying hens. Physiol. Behav., 55: 313–316.

Hubrecht, R.C., 1993. A comparison of social and environmental enrichment methods for laboratory housed dogs. Appl. Anim. Behav. Sci., 37: 345–361.

Hughes, B.O. and Duncan, I.J.H., 1988. The notion of ethological "need", models of motivation and animal welfare. Anim. Behav., 36: 1696–1707.

Jensen, P. and Toates, F.M., 1993. Who needs "behavioural needs"? Motivational aspects of the needs of animals. Appl. Anim. Behav. Sci., 37: 161–181.

Jones, R.B. and Waddington, D., 1992. Modification of fear in domestic chicks, *Gallus gallus domesticus*, via regular handling and early environmental enrichment. Anim. Behav., 43: 1021–1033.

Kastelein, R.A. and Wiepkema, P.R., 1989. A digging trough as occupational therapy for Pacific Walruses (*Odobenus rosmarus divergens*) in human care. Aquat. Mammals, 15: 9–17.

King, J.E. and Norwood, V.R., 1989. Free-environment rooms as alternative housing for squirrel monkeys. In: E. Segal (Editor), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, Park Ridge, NJ, pp. 102–114.

Konovalov, V.V., 1986. Hygienic evaluation of machinery noise in poultry houses. Veterinariya, Moscow, 10: 23–25.

Ladd, J.K., Albright, J.L., Beck, A.M. and Ladd, B.T., 1992. Behavioral and physiological studies on the effect of music on animals. J. Anim. Sci. 70 (Suppl. 1): 170.

Lawrence, A.B. and Terlouw, E.M.C., 1993. A review of behavioral factors involved in the development and continued performance of stereotypic behaviors in pigs. J. Anim. Sci., 71: 2815–2825.

Love, J.A., 1994. Group housing: meeting the physical and social needs of the laboratory rabbit. Lab. Anim. Sci., 44: 5–11.

Markowitz, H. and Line, S., 1989. Primate research models and environmental enrichment. In: E. Segal (Editor), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, Park Ridge, NJ, pp. 203–212.

Mason, G.J., 1991. Stereotypies and suffering. Behav. Proc., 25: 103–115.

Mastika, I.M. and Cumming, R.B., 1987. Effect of previous experience, and environmental variations on the performance and pattern of feed intake of choice fed and complete fed broilers. In: D.J. Farrell (Editor), Recent Advances in Animal Nutrition in Australia 1987. University of New England, Armidale, pp. 260–282.

McFarland, D., 1989. Problems of Animal Behaviour. Longman, Harlow, UK.

McGlone, J.J. and Curtis, S.E., 1985. Behavior and performance of weanling pigs in pens equipped with hide areas. J. Anim. Sci., 60: 20–24.

Mench, J.A., 1995. Environmental enrichment: mandate in search of a theory. In: D. Shepherdson and J. Mellen (Editors), Zoo Environmental Enrichment. Smithsonian Press, in press.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Calvo, L., Hanebury, L. and Wharton, T., 1990. Development of survival skills in captive-raised Siberian polecats (*Mustela eversmanni*) II: Predator avoidance. J. Ethol., 8: 95–104.

Mononen, J., Harri, M., Rouvinen, K. and Niemel, P., 1993. The use of resting platforms by young silver foxes (*Vulpes vulpes*). Appl. Anim. Behav. Sci., 38: 301–310.

Moodie, E.M. and Chamove, A.S., 1990. Brief threatening events beneficial for captive tamarins? Zoo Biol., 9: 275–286.

Newberry, R.C., 1993. The space–time continuum, and its relevance to farm animals. Etologia, 3: 219–234.

Newberry, R.C. and Wood-Gush, D.G.M., 1988. Development of some behaviour patterns in piglets under semi-natural conditions. Anim. Prod., 46: 103–109.

Newberry, R.C., Wood-Gush, D.G.M. and Hall, J.W., 1988. Playful behaviour of piglets. Behav. Proc., 17: 205–216.

Nicol, C.J., 1992. Effects of environmental enrichment and gentle handling on behaviour and fear responses of transported broilers. Appl. Anim. Behav. Sci., 33: 367–380.

Nørgaard-Nielsen, G., Vestergaard, K. and Simonsen, H.B., 1993. Effects of rearing experience and stimulus enrichment on feather damage in laying hens. Appl. Anim. Behav. Sci., 38: 345–352.

Novak, M.A. and Drewson, K.H., 1989. Enriching the lives of captive primates: issues and problems. In: E. Segal (Editor), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, Park Ridge, NJ, pp. 161–182.

Ogden, J.J., Lindburg, D.G. and Maple, T.L., 1994. A preliminary study of the effects of ecologically relevant sounds on the behaviour of captive lowland gorillas. Appl. Anim. Behav. Sci., 39: 163–176.

O'Neill, P., 1989. A room with a view for captive primates: issues, goals, related research and strategies. In: E. Segal (Editor), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, Park Ridge, NJ, pp. 135–160.

Pearce, G.P. and Paterson, A.M., 1993. The effect of space restriction and provision of toys during rearing on the behaviour, productivity and physiology of male pigs. Appl. Anim. Behav. Sci., 36: 11–28.

Pereira, M.E., Macedonia, J.M., Haring, D.M. and Simons, E.L., 1989. Maintenance of primates in captivity for research: the need for naturalistic environments. In: E. Segal (Editor), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, Park Ridge, NJ, pp. 40–60.

Reed, H.J., Wilkins, L.J., Austin, S.D. and Gregory, N.G., 1993. The effect of environmental enrichment during rearing on fear reactions and depopulation trauma in adult caged hens. Appl. Anim. Behav. Sci., 36: 39–46.

Reinhardt, V., 1994. Caged rhesus macaques voluntarily work for ordinary food. Primates, 35: 95–98.

Robert, S., Matte, J.J., Farmer, C., Girard, C.L. and Martineau, G.P., 1993. High-fibre diets for sows: effects on stereotypies and adjunctive drinking. Appl. Anim. Behav. Sci., 37: 297–309.

Rumbaugh, D.M., Washburn, D. and Savage-Rumbaugh, E.S., 1989. On the care of captive chimpanzees: methods of enrichment. In: E. Segal (Editor), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, Park Ridge, NJ, pp. 357–375.

Rushen, J., 1984. Stereotyped behaviour, adjunctive drinking and the feeding periods of tethered sows. Anim. Behav., 32: 1059–1067.

Schaefer, A.L., Salomons, M.O., Tong, A.K.W., Sather, A.P. and LePage, P., 1990. The effect of environmental enrichment on aggression in newly weaned pigs. Appl. Anim. Behav. Sci., 27: 41–52.

Scott, T.A. and Balnave, D., 1988. Comparison between concentrated complete diets and self-selection for feeding sexually-maturing pullets at hot and cold temperatures. Br. Poult. Sci., 29: 613–625.

Shepherdson, D., 1994. The role of environmental enrichment in the captive breeding and re-introduction of endangered species. In: G. Mace, P. Olney and A. Feistner (Editors), Creative Conservation: Interactive Management of Wild and Captive Animals. Chapman and Hall, London, pp. 167–175.

Shepherdson, D., Bemment, N., Carman, M. and Reynolds, S., 1989a. Auditory enrichment for Lar gibbons *Hylobates lar* at London Zoo. Int. Zoo Yearb., 28: 256–260.

Shepherdson, D., Brownback, T. and James, A., 1989b. A meal worm dispenser for the Slender-tailed meerkat (*Suricata suricatta*) at London Zoo. Int. Zoo Yearb., 28: 268–271.

Shepherdson, D.J., Carlstead, K., Mellen, J.D. and Seidensticker, J., 1993. The influence of food presentation on the behavior of small cats in confined environments. Zoo Biol., 12: 203–216.

Simonsen, H.B., 1990. Behaviour and distribution of fattening pigs in the multi-activity pen. Appl. Anim. Behav. Sci., 27: 311–324.

Snowdon, C.T. and Savage, A., 1989. Psychological well-being of captive primates: general considerations and examples from callitrichids. In: E. Segal (Editor), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, Park Ridge, NJ, pp. 75–88.

Steinruck, U., Kirchgessner, M. and Roth, F.X., 1990. Selective methionine intake of broilers by changing the positions of the diets. Arch. Geflugelkd., 54: 245–250.

Stolba, A. and Wood-Gush, D.G.M., 1989. The behaviour of pigs in a semi-natural environment. Anim. Prod., 48: 419–425.

Terlouw, E.M.C., Lawrence, A.B. and Illius, A., 1991. Influences of feeding level and physical restriction on the development of stereotypies in sows. Anim. Behav., 42: 981–991.

Ulrich, R., 1984. View through a window may influence recovery from surgery. Science, 224: 420.

Von Borell, E. and Hurnik, J.F., 1990. Stereotypic behavior and productivity of sows. Can. J. Anim. Sci., 70: 953–956.

Wemelsfelder, F., 1991. Animal boredom: do animals miss being alert and active? In: M.C. Appleby, R.I. Horrell, J.C. Petherwick and S.M. Rutter (Editors), Applied Animal Behaviour: Past, Present and Future. U.F.A.W., Potters Bar, UK, pp. 120–123.

Widman, D.R., Abrahamsen, G.C. and Rosellini, R.A., 1992. Environmental enrichment: the influences of restricted daily exposure and subsequent exposure to uncontrollable stress. Physiol. Behav., 51: 309–318.

Wood-Gush, D.G.M. and Vestergaard, K., 1989. Exploratory behavior and the welfare of intensively kept animals. J. Agric. Ethics, 2: 161–169.

Wood-Gush, D.G.M. and Vestergaard, K., 1991. The seeking of novelty and its relation to play. Anim. Behav., 42: 599–606.

Young, R.J., Carruthers, J. and Lawrence, A.B., 1994. The effect of a foraging device (the "Edinburgh Foodball") on the behaviour of pigs. Appl. Anim. Behav. Sci., 39: 237–247.