Environmental Enrichment for Laboratory Rodents: Animal Welfare and the Methods of Science

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Because of the difficulty of establishing objective measures of laboratory rodents' psychological well-being, developing environmental enrichment programs that are actually beneficial to rodents destined to participate in laboratory research is particularly challenging. Many studies of effects of environmental complexity, social housing, and increases in cage size suggest that professional judgments as to the impact of diverse types of environmental enrichment on rodent welfare are not a reliable basis for evaluating the outcomes of enrichment programs for laboratory rodents. Successful enrichment programs will vary from one rodent species to another, between sexes, as well as between age classes. There is a need for objective, measurable goals for proposed environmental enrichment programs for rodents, as well as for empirical investigations of the beneficial and detrimental consequences of proposed environmental manipulations.

Improving the welfare of rodents destined to participate in laboratory research by enrichment poses challenges that often do not arise when enriching the maintenance environments of nonhuman animals kept for other purposes. If, for example, members of an endangered species are held in captivity with the intention of eventually releasing their progeny into natural habitat, at least in principle, it is easy to determine whether an environmental enrichment program has been successful. If some change in the captive environment increases the probability that a released individual survives and reproduces in natural circumstances, then enrichment has been successful. The probability of survival and re-

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production of released individuals provides a clearly stated, objective measure of success or failure of the enrichment program.

Similarly, clear objective goals of environmental enrichment programs for animals held in zoos can often be specified. Such goals include suppression of self-destructive or stereotypic patterns of behavior, maintenance of the natural behavioral repertoire of captive animals, and increased rates of reproduction. Unfortunately, it is often considerably more difficult to determine whether changes in the maintenance environment of purpose-bred laboratory rodents, that often do not exhibit overt symptoms of psychological distress, have actually accomplished anything other than to increase the costs of research.

Veterinary measures of the welfare of laboratory rodents—indices of injury, disease, dehydration, and starvation—are objective and relatively straightforward. It is far more difficult to determine whether some manipulation enhances the psychological welfare of laboratory rodents, which is the goal of most environmental enrichment procedures.

Unfortunately, there are no agreed-on measures of the psychological health of laboratory rodents. Rats and mice do not wag their tails when they are happy. They do not have facial expressions, vocalizations, or postures indicative of positive psychological states. Consequently, once the parameters of the physical environment and schedules of cleaning have been arranged in a satisfactory manner, it is hard to tell whether the psychological well-being of a rat, mouse, or other rodent is unsatisfactory. It is, therefore, difficult to know whether some change in a maintenance environment improves the psychological well-being of its rodent inhabitants. The probability of increasing rodents’ welfare by environmental enrichment is, therefore, greatly diminished.

Our professional judgments or intuitions as to what changes in the physical or social environment increase rodents’ psychological welfare are less accurate than we might hope. All too frequently, empirical studies, undertaken to measure effects of environmental enrichment on laboratory rodents, reveal significant gaps in our knowledge of how to enrich rodents’ environments in ways that are actually beneficial to the animal.

Table 1 lists some of the many environmental enrichment procedures and indices of animal well-being proposed in the literature. Both were extracted from Shepardson, Mellen, and Hutchin’s (1998) recent edited volume on environmental enrichment. The items marked with a superscript in Table 1 are those that are touched on in this article.

<table>
<thead>
<tr>
<th>Types of Environmental Enrichment</th>
<th>Potential Goals of Environmental Enrichment</th>
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<tbody>
<tr>
<td>Increased environmental complexity*</td>
<td>More natural behavior*</td>
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<td>Increased cage size</td>
<td>Maintenance of species typical repertoire*</td>
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<tr>
<td>Providing social companionship*</td>
<td>Not fearful*</td>
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<tr>
<td>Providing “control” or intellectual challenge</td>
<td>Absence of abnormal behaviors*</td>
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<td>Rests in a relaxed manner*</td>
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<td>Improved health*</td>
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<td>Greater resistance to disease organisms*</td>
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<td>Increased reproduction*</td>
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<td>Reduced cortisol levels</td>
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<td>Greater psychological well-being*</td>
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<td>Opportunities for achievement</td>
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<td>Unpredictability and novelty*</td>
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<td>Opportunities to explore and gain</td>
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<td>information about the environment</td>
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<td>Opportunities for social interaction*</td>
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I have not provided a comprehensive review of the literature. Rather, I have selected studies and observations to discuss that seem to me to raise important issues related to effects of environmental enrichment on the well-being of rodents housed in laboratory cages.

MAINTAINING BEHAVIORAL REPERTOIRES OF LABORATORY RODENTS

More than 20 years experience with “wild” rats (Rattus norvegicus and Rattus rattus), house mice (Mus musculus), and other less-familiar rodents (such as grasshopper mice and kangaroo rats) leads me to conclude it is not desirable to maintain laboratory rodents the full range of behaviors seen in their wild progenitors. Wild rodents are often difficult, even dangerous, to handle. When they have to undergo even the least invasive of laboratory procedures such as movement from a holding cage to
an experimental apparatus, they exhibit every sign of extreme distress. They bite, scream, urinate, and defecate. One goal of the laboratory environment for rodents must be to maintain the docility, placidity, and tameness that characterize the domesticated behavioral phenotype of laboratory rodents.

Domestication: A Genotype x Environment Interaction

It might be argued that domesticated animals have domesticated genes and will grow up to be tame and docile, however you maintain them. The domesticated phenotype can, however, be the result of a genotype–environment interaction (the development of a domesticated genotype in a domestic environment). Consequently, raising a genetically domestic rodent in a wild-type environment may produce a wild behavioral phenotype unsuited to life in the laboratory.

Environmental Complexity

More than 20 years ago, before environmental enrichment was an issue, Clark and Galef (1977, 1979, 1980, 1981) conducted a series of studies to determine the requisite conditions for development of tameness in the domesticated Mongolian gerbil (Meriones unguiculatus). Gerbils are normally docile creatures, often touted (albeit inappropriately) as ideal pets for children.

Clark and I allowed gerbils reared in standard laboratory cages to rear their own young in burrow systems they constructed in large enclosures filled with earth (Clark & Galef, 1977). We found that pairs of burrowing adults remained tame and easy to handle. They would come out of their burrows when they heard someone enter the room containing their enclosures. We could reach into an enclosure and pick up its residents. On the other hand, young born and reared in the enriched environment constructed by their parents were very hard to catch (we had to use live traps to capture them), and they were very resistant to handling. They bit and tried to escape when held (Clark & Galef, 1977). They were also unusually susceptible to epileptiform seizures either when picked up or when placed in an open area (Clark & Galef, 1981).

We went on to explore the environmental variables that caused this ferailization of the behavior of genetically domesticated gerbils who had been reared in a burrow. We discovered that providing young gerbils (Clark & Galef, 1977) with a shelter in which to hide produced many of the same behavioral characteristics as did early life in a burrow (Figure 1). As we progressed from rearing gerbil young in an open laboratory cage (not illustrated in Figure 1), to rearing them in an open cage that permitted movement in three dimensions (Figure 1a), to a cage with a partition with a hole in it (Figure 1b), to a cage providing access to shelter (Figure 1c), to a cage providing both a three-dimensional substrate and access to shelter (Figure 1d), to a tunnel constructed by adult gerbils, we saw a steady increase in flight responses to the approach of humans (Clark & Galef, 1977).

It was not just the gerbils' behavior that changed in response to rearing conditions. As shown in Figure 2, gerbils reared with access to shelter had substantially larger adrenal-weight to body-weight ratios than did gerbils reared in standard laboratory cages. Gerbils reared in cages providing shelter also had smaller reproductive organs and heavier pituitary glands than did gerbils reared in standard laboratory cages (Clark & Galef, 1980, 1981). Thus, by enriching the animals' environment during infancy and adolescence (Clark & Galef, 1979), we had produced modifications in behavior and physiology that might be desirable in rodents intended for reintroduction into the wild or even for zoos that wanted to display animals with intact behavioral repertoires. These same gerbils were, however, obviously inappropriate for use in the usual sort of laboratory studies. Environmental enrichment increased the distress that the gerbils experienced whenever they had to encounter human care.
3.5 cm. The cost of buying new cages for all rats, even in a small country like Canada, must have been tens of millions of dollars, to say nothing of the ongoing increase in the cost of replacing, cleaning, and providing animal-room space for the larger cages. I thought it might be worthwhile, before my department bought $100,000 worth of new rat cages, cage lids, racks for cages, and equipment for the cage washer, to ask whether Norway rats were more comfortable in cages of the new height than of the old.

Because laboratory rats are fairly recently derived from wild Norway rats who, for many millions of years, spent most of their lives in subterranean burrows, it seemed possible that members of domesticated strains of Norway rats might actually prefer shorter cages to taller ones. The burrows of wild Norway rats consist of tunnels averaging only 7.5 cm in height that connect nest chambers averaging only 14.5 cm high (Calhoun, 1962). If rats respond to their laboratory cages as if they were nest chambers, then the old, 16.8-cm cages might actually be too tall, not too short, for maximizing rats’ psychological comfort.

So: a colleague and I (Galef & Durlach, 1993) undertook a fairly straightforward experiment, modeled on experiments performed with battery-reared hens at Oxford University in the United Kingdom (Dawkins, 1977, 1998). We reasoned that if rats found a 16.8-cm-high cage in any way less comfortable than a 20-cm-high cage, then, when given a choice between cages of the two heights, they would spend more time in the more comfortable, taller cage than in the less comfortable, shorter one.

We housed our 8 subjects, all large male domesticated rats of the Long–Evans or Sprague–Dawley strain, individually in the apparatus illustrated in Figure 3. The apparatus was simply two cages of different heights joined by a piece of polyvinyl chloride (PVC) tubing 7.5 cm in diameter. Subjects were left undisturbed in the apparatus for 5 or 6 days to habituate to their new home, then were videotaped using a time-lapse video recorder for 24 hr. Each videotape was scored by two observers who determined independently what percentage of the time each rat spent in the taller cage.

As can be seen in Figure 3, large, male Long–Evans rats spent, on average, 54.7% of the 24-hr test period in the taller cage, and only 5 of the 8 subjects preferred the tall side of the apparatus to the short side. Clearly, the rats exhibited no preference between tall and short cages that was statistically meaningful.

Our results failed to provide support for the hypothesis that rats were less comfortable when held in shorter cages than when held in taller ones. They are consistent with the results of studies of various species of macaque that have found little or no effect of cage size on several physiological and behavioral measures of distress (Bayne & McCully, 1989; Crockett et al., 1993a, 1993b; Crockett, Yamashiro, DeMers, & Emerson, 1996). Cage size may not be a particularly important environmental contributor to the well-being of laboratory animals in general, and increasing cage height may not be a particularly appropriate way to expend finite resources in the attempt to increase the welfare of laboratory rats.


**TABLE 1**

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<tr>
<th>Cagesize</th>
<th>Standard cage</th>
<th>Cage with shelter</th>
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<tbody>
<tr>
<td>Height</td>
<td>16.8 cm</td>
<td>20 cm</td>
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<tr>
<td>AGE IN DAYS</td>
<td>15</td>
<td>20</td>
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Some years ago in Canada, where I work, the Canadian Council on Animal Care mandated that all rats should be kept not in the 16.8-cm-high cages then standard in Canadian laboratories, but in cages 20 cm in height. That is, the Council insisted that the height of cages in which rats of all ages were to be kept should be increased by

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**CAGE SIZE**

A second kind of enrichment intended to increase the welfare of laboratory rodents involves increasing the size of the animals’ cages. Although the issue may seem trivial, even if having larger cages does not benefit animals, it’s hard to imagine that increasing the size of their cages harms them in any way. However, committing limited resources to providing animals with larger cages can be harmful if it reduces resources available for other aspects of animal care.

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ENVIROMENTAL ENRICHMENT FOR LABORATORY RODENTS

The results of these informal observations suggest that individual rats actually avoid the PVC tubes; certainly the frequency with which rats housed individually are found inside PVC tubes is far less than one would expect if the animals simply distributed themselves randomly about the floors of their cages. The observation that one member of a pair of rats is more likely to be seen in a tube than is a rat living alone is consistent with the hypothesis that submissive members of pairs take refuge from the attentions of their cage mates in the tubes. Further work would be needed, however, to determine whether the same member of a pair always uses the tube in its cage and whether that animal is the submissive or dominant member of its pair. We intend to undertake such investigations in the near future.

One negative consequence of introducing 15-cm lengths of PVC tubing into the cages of individually housed rats is the reduction of the effective floor space of the cage. Whether any benefit accrues to rats provided with a piece of PVC tubing remains to be determined.

SOCIAL ENRICHMENT

There also is not much evidence that laboratory rodents are better off when housed with a conspecific than when caged alone. When two rodents are placed together in a cage, one will become dominant to the other. It is possible, though surely not certain, that a dominant animal might experience some increase in its psychological well-being because of the presence of a subordinate. However, it seems at least as likely that a subordinate, unable to avoid constant interaction with its superior (as it would outside the captive environment; Calhoun, 1962), would suffer appreciable reduction in its psychological well-being. There is indeed some data suggesting that, in at least two rodent species, social housing may have detectable negative consequences.

Figure 4 (Klein & Nelson, 1999) shows that the immune system of male meadow voles (Microtus pennsylvanicus) is suppressed by housing animals in same-sex pairs. Such statistically significant effects were not found either in female meadow voles or in prairie voles (Microtus ochrogaster) of either sex. Figure 5 shows that corticosterone levels are significantly elevated in female prairie voles housed in same-sex pairs, but not in either male prairie voles or in meadow voles housed in either same- or mixed-sex pairs.

The details are not important. What is important is that there are differences in the responses to different types of social enrichment of each species, each sex, and perhaps (though no data is available) each age class. The dissociation of immune-system and corticosterone responses to social enrichment also challenges the view that corticosterone levels provide an adequate measure of distress. The bottom line is that animals should be kept under rather different maintenance re-

GENERAL DISCUSSION

What messages do I draw from all of this? First, and most important, we need agreed-on, clearly stated, objective criteria for measuring changes in the psychological well-being of laboratory rodents. Second, we need to determine the effects of proposed procedures for environmental enrichment on such indices of psychological health. We need to apply the scientific method to questions of animal welfare. The scientific enterprise requires that the meaning of various consequences of manipulations be defined before those manipulations are carried out, and that the consequences of manipulations are measured objectively.

I have suggested that maintenance of the tame, docile behavior characteristic of laboratory rodents may be one such criterion of a successful maintenance environment. In the laboratory environment, contact with humans is a frequent occurrence. Animals who show low levels of reactivity may be more comfortable than those who show high levels of reactivity to such contact. Whatever the criteria that are to serve as indices of increased psychological well-being, they must be objectively measurable.

We also require precise specification of what constitutes success and failure, to guard against the inherent unreliability of professional judgments of the value of interventions. The inadequacy of professional judgments for determining the effectiveness of medical interventions is well established (Gilovich, 1991). Because of such inadequacy, contemporary medical procedures require double-blind experimental designs and random assignment of subjects to conditions. Professional judgments are no more satisfactory as a means of establishing the efficacy of treatments when patients are animals than when they are humans. We need to recognize the need for well-designed, carefully conducted and analyzed empirical research to determine which changes in the maintenance environment provided for laboratory rodents actually move us toward whatever objectively measurable goals we have specified. We need to undertake the requisite studies.

Finally, we need to recognize that optimal environments are likely to vary from one species to another, from one sex to the other, and from age class to age class.

If our attempts to enrich the maintenance environments of laboratory animals is simply part of a public relations exercise, then of course we can proceed without accomplishing anything. However, if our goal is actually to improve the lives of the animals in our charge, then we need to measure the effects of alternative maintenance environments on the psychological distress arising from captivity. Appeals to intuition, professional judgment, or poorly substantiated or narrowly held theories (Weihe, 1987) are not adequate bases for decisions concerning the well-being of laboratory rodents. Indeed, enrichment programs based on unscientific belief systems or unscientific methods must be counterproductive in the end. Good will toward animals plus professional judgment is simply not enough. We need to undertake research on the efficacy of whatever enrichment procedures we propose to implement. If we do not, we are not meeting our moral obligations, either to the animals who participate in scientific research or to the public that asks that we treat our animals as humanely as we can and spend public funds wisely.

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REFERENCES


In the last 50 years, there has been a growing need for storage and management systems for the production and maintenance of large numbers of dogs. Unwanted dogs and strays, detained in kennels, stay for various lengths of time. Large kennels also produce dogs for sale as companion animals, for the service dog industry (police and guide dogs), for biomedical research, and for use by dog food companies. Across the United States, literally tens of thousands of dogs are born in kennels and spend their lives in kennels. The laboratory dog, the kennel dog, the service dog, and the companion dog are in an evolutionary transition period, accompanied by concomitant adaptation to stresses signaled by a high frequency of genetic disease and behavioral abnormalities. For kennel enrichment programs, such as socialization and exercise, the modern kennel-raised dog is a genetically moving target. Specific recommendations apply neither to all breeds nor to the variations within a single breed.

Fifty years ago, far fewer dogs were kept in kennels. The various dog industries were either nonexistent or much smaller, and dogs were more often handled on an individual basis. Because of the recent population increase, dogs have had to adapt genetically—both physically and behaviorally—to new systems of husbandry. Although the main goal for working-dog breeders and sports people has always been to develop fine working-animals (sheep, sled, and racing dogs), modern kennel industries have overlooked their techniques of group kenneling socialization of young dogs, and exercising of working animals. With the exception of the service dog industry, rarely is the modern kennel-raised dog expected to do anything except, in some sense, be a generic dog. Like most modern, companion-animal dog breeds, the laboratory beagle is simply a historical represen...