JOURNAL OF APPLIED ANIMAL WELFARE SCIENCE, 2(4), 267–280

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

Bennett G. Galef, Jr.
Department of Psychology
McMaster University

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-

Requests for reprints should be sent to Bennett G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, Ontario, Canada L8S 4K1. E-mail: galef@mcmaster.ca

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 Sheperdson, 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.

I have two goals: (a) to describe some unexpected consequences of well-intentioned attempts to increase the welfare of laboratory rodents by changing the physical or social environment in which the animals were maintained, and (b) to suggest that without objective research on the consequences of enrichment procedures, attempts to improve the welfare of animals by enriching their environments are unlikely to succeed.

TABLE 1
Types of Environmental Enrichment and Potential Goals of Environmental Enrichment

Types of Environmental Enrichment
Increased environmental complexity[a]
Increased cage size[a]
Providing social companionship[a]
Providing "control" or intellectual challenge
Goals of Environmental Enrichment
More natural behavior[a]
Maintenance of species typical repertoire[a]
Not fearful[a]
Absence of abnormal behaviors[a]
Rests in a relaxed manner[a]
Improved health[a]
Greater resistance to disease organisms[a]
Increased reproduction[a]
Greater longevity
Reduced cortisol levels[a]
Greater psychological well-being[a]
Opportunities for achievement
Unpredictability and novelty[a]
Opportunities to explore and gain information about the environment
Opportunities for social interaction[a]

[a]Items discussed in the text.

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 in 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 × 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 feralization 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

Rearing Environment	*Percent Fleeing When Approached*
Standard cage	57.6
Three-dimensions (A)	50.0
Partition and opening (B)	76.9
Shelter (C)	84.6
Three-dimensions and shelter (D)	92.3
Tunnel	100.0

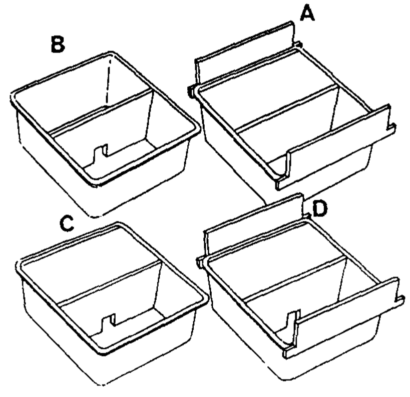

FIGURE 1 Enclosures used to examine environmental effects on Mongolian gerbils' response to the approach of humans and effects of those environments on a gerbil's tendency to flee. Enclosures providing (A) access to a three-dimensional substrate, (B) a partition with an opening through which to run, (C) access to shelter, and (D) both access to shelter and a three-dimensional substrate. *Note.* From "The Role of the Physical Rearing Environment in the Domestication of the Mongolian Gerbil," by M. M. Clark & B.G. Galef, 1977, *Animal Behaviour, 25*, p. 304. Copyright 1977 by Academic Press. Adapted with permission.

(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-

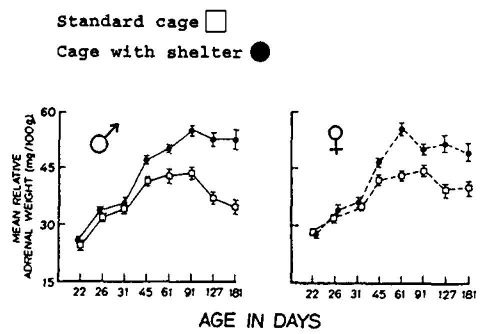

FIGURE 2 Effects of rearing in standard laboratory cages and in gerbil-constructed tunnel systems on the adrenal weight to body weight ratios of male and female gerbils. Flags + 1 SEM. *Note.* From "Effects of Rearing Environment on Adreal Weights, Sexual Development, and Behavior in Gerbils: An Examination of Richter's Domestication Hypothesis," by M. M. Clark & B. G. Galef, 1980, *Journal of Comparative Psychology, 94,* p. 860. Copyright 1980 by the American Psychological Association. Adapted with permission.

takers or experimenters. Thus, environmental enrichment had measurable negative consequences, in addition to whatever positive consequences it may have had.

Does the same decrease in suitability for laboratory life result when Norway rats or house mice are reared in a more natural environment than that provided by a barren laboratory cage? So far as I know, no one has carried out the necessary experiments, though Boice (1977) did mention in passing in an article concerned with burrowing by rats that "rats raised underground were more reactive to laboratory events than those raised above ground" (p. 657). Those who have had rats or mice escape from their cages and spend a day or two at liberty on the animal-room floor (which can, I suppose, be thought of as a highly enriched environment) know that the experience of life on the loose produces a transitory increase in the timidity and emotionality of escapees.

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.

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

about 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.

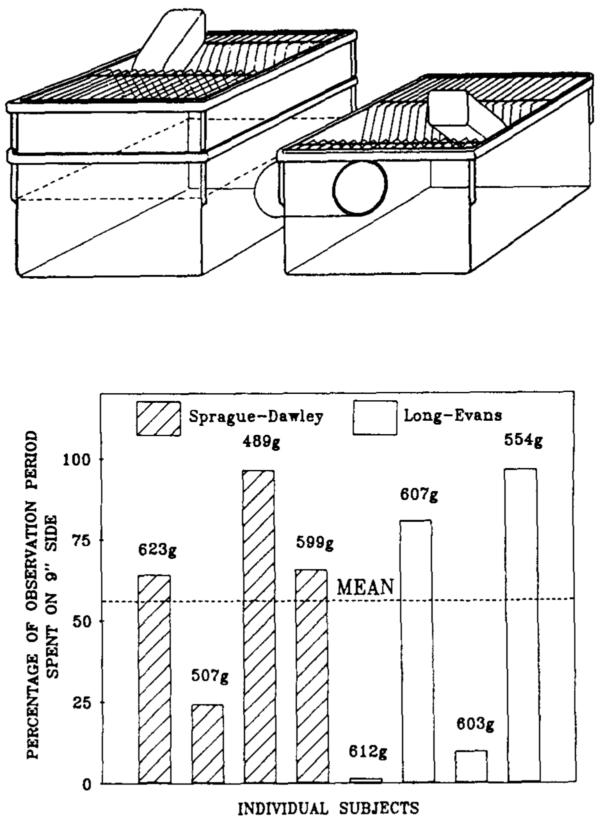

FIGURE 3 Apparatus used to examine effects of cage height on cage utilization by Norway rats, and percentage of 24 hr each of 8 rats spent on the higher side of the apparatus. Numbers above each histogram indicate the weight of each subject. *Note.* From "Should Large Rats Be Housed in Large Cages?" by B. G. Galef & P. Durlach, 1993, *Canadian Psychology, 34,* pp. 205–206. Copyright 1993 by the Canadian Psychological Association. Reprinted with permission.

PROVISION OF PVC SHELTERS

Those of us working in Canada are strongly encouraged to provide rats with lengths of PVC tubing that allow rats to conceal themselves within the transparent cages in which we are required to house them. I have kept informal records of the frequency with which adult Norway rats, housed either in isolation or in pairs, make use of the 15-cm long, 7.5-cm diameter PVC shelters with which they are provided. I examined 125 cages containing a single rat and a length of PVC tubing. I found only 5 of

the animals in their shelters. On the other hand, 13 of the 76 animals kept in pairs were in their PVC tubes when I examined their cages.

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-

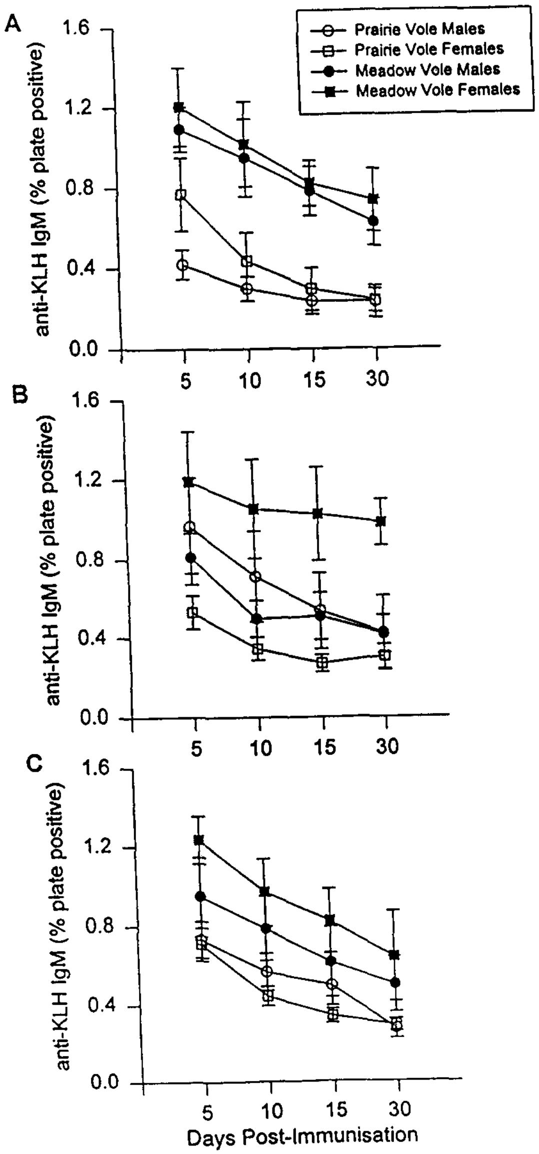

FIGURE 4 Immune system response of male and female, prairie and meadow voles housed either (A) individually or in (B) same- or (C) mixed-sex pairs. *Note.* From "Social Interactions Unmask Sex Differences in Humoral Immunity in Voles," by S. L. Klein & R. J. Nelson, 1999, *Animal Behaviour, 57,* pp. 606–607. Copyright 1999 by Academic Press. Reprinted with permission.

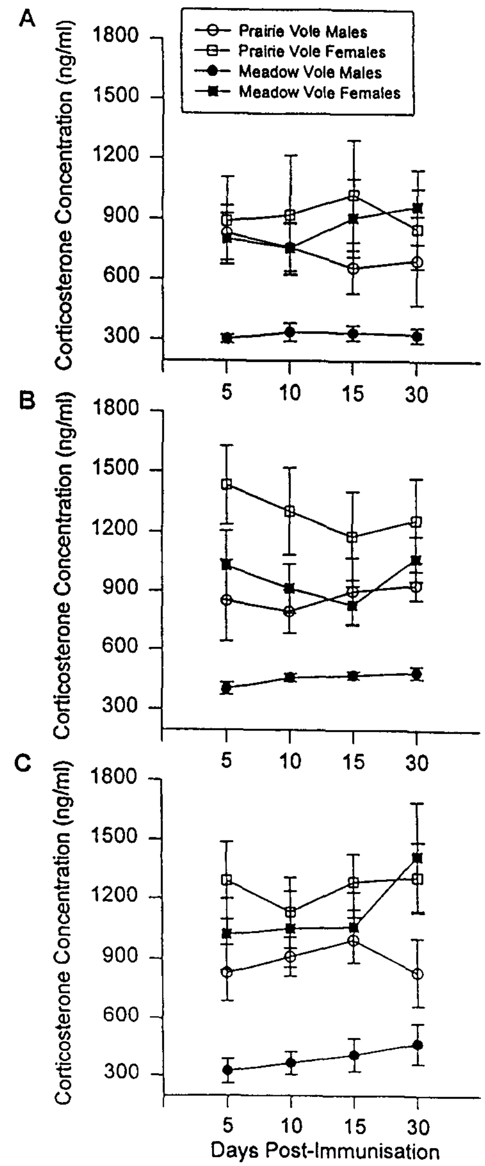

FIGURE 5 Corticosterone levels of male and female, prairie and meadow voles housed either (A) individually or in (B) same- or (C) mixed-sex pairs. *Note.* From "Social Interactions Unmask Sex Differences in Humoral Immunity in Voles," by S. L. Klein & R. J. Nelson, 1999, *Animal Behaviour, 57,* pp. 606–607. Copyright 1999 by Academic Press. Reprinted with permission.