As described in the introduction of this thesis one of the main goals of environmental enrichment is to provide animals with opportunities to better perform their species-specific behaviour, thereby implying that in this way their welfare is enhanced (Beaver 1989; Benn 1995; Chamove 1989a; Hart 1994; Markowitz & Gavazzi 1995; Mench 1994; Poole 1988; Scharmann 1991). But how can the welfare implication of enrichment be established?

The use of preference tests to evaluate the effect of environmental enrichment is based on the assumption that natural selection has shaped the decision-making process of animals in such a way that the resultant behaviour sequences are optimally adapted to the current environmental circumstances (Fraser 1996; McFarland 1977). What the impact of these choices on the welfare status is, cannot be measured directly, therefore we have to use indirect ways and a range of measures to evaluate the welfare status of the animal. By using behavioural and physiological parameters, it is possible to measure the effects of (enriched) environmental conditions. Interpretation of such effects in terms of animal welfare is done against the background of other experimental data and theoretical or philosophical assumptions (Sandøe & Simonsen 1992). The assumption that animals will choose those circumstances in which they feel 'good', is based on the analogy postulate. This postulate assumes that humans and animals which are comparable with regard to many aspects of their physiology and anatomy, are also comparable with regard to the ability of experiencing pain and distress (Stafleu et al 1992). This line of reasoning may also allow to conclude that an animal experiences it as positive to achieve the objective it is willing to work for, and that by attaining this objective its welfare is improved (Broom 1988; Van Rooijen 1983/84). On the other hand, the impossibility to perform certain behaviour may increase the effects of stressful situations and cause suffering (Jensen & Toates 1993). Environments which allow animals to perform more of the natural behavioural repertoire, also allow a larger range of behavioural choices and may thus enhance the well-being of the animals.

Poole (1992) is questioning whether the provision of a single object can be considered as environmental enrichment, since enrichment should allow the performance of a complex behavioural repertoire. This is provoking the question whether the term enrichment is sufficiently defined. Ruschen (1995, Applied Ethology Discussion List, Internet) prefers the term environmental improvement instead of enrichment and divides the animal’s environmental requirements into those that are essential and those that are beneficial. Others prefer environmental modification as a more neutral term. According to Duncan (1995, Applied Ethology Discussion List, Internet) environments should allow the performance of essential
species-specific behaviours, which he regards as an essential design feature and not as environmental enrichment. Newberry (1995) has doubts about the use of the term enrichment because it implies improvement, whereas the term is frequently used for the process of environmental change whatsoever. According to her views, the term should be applied only to the (successful) outcome of these environmental changes. It is easy to qualify any improvement to the current barren environments we provide for animals as enrichment, but from a scientific point of view enrichment is about discussing motivation and the effects of frustrating or satisfying these motivations (De Passillé 1995, Applied Ethology Discussion List, Internet). At present, the term enrichment covers a range of modifications of the environment, from satisfying a strong motivation (behavioural need) to making things more interesting for the animals. It seems useless trying to find a term which covers the whole process currently considered as environmental enrichment, since this term is already used widespread in the literature. But it seems making sense to restrict its use to those environmental changes for which animals choose in a preference test and/or of which the positive effects have been shown.

The need of environmental enrichment for laboratory animals is questioned by Beilharz (1994). According to him laboratory animals such as rats and mice do not need an extremely complex environment because they should become adapted to simple laboratory environments in which they are less costly to maintain. Beilharz assumes that the behaviour of these animals quickly adapts genetically to the captive environments. However, as was shown by Van Oortmerssen (1971), laboratory mice do not demonstrate strain-specific, functional adaptations to the artificial laboratory environment. The behavioural differences which he found between inbred strains, have originated in nature as adaptations to different biotopes before the strains became domesticated. Animals with complex, flexible behaviour can adapt to most environments without a change of their genotypes. The entire behavioural repertoire described for wild mice still occurs in laboratory mice, provided that they are given the appropriate environment to live in (Van Oortmerssen 1971).

Adams & Boice (1981) and Boice (1977) showed that the burrowing activities of wild and laboratory rats and mice of inbred strains were similar in every regard, including dimensions and sequence of construction. Burrowing behaviour is comparable to nest making, the movements used in both activities are rather similar (Brain & Rajendram 1986). In the study described in Chapter 3 of this thesis, mice which had never been in contact with nesting materials were allowed to choose between cages with nesting materials or a cage without nesting material similar to the one in which they were housed since weaning. They all preferred a cage with nesting material and within a few hours they constructed a
nest. Other authors have reported the start of nest building activities even within minutes after nesting material was put in the home cages of laboratory mice (Schneider & Chenoweth 1970; Van Oortmerssen 1971; Watson 1993).

All these reports suggest that laboratory mice and rats, despite inbreeding, still have complex behavioural abilities which are not very different from their wild counterparts. Thus it seems warranted to look more closely to current laboratory housing systems and to seek for adaptations that can meet the natural behavioural requirements in a better way.

In this thesis emphasis is put on the evaluation of simple adaptations of existing housing systems. Preference tests were used as one of the tools to evaluate these enrichments. The preferences of mice for two different types of enrichments were determined: one which could satisfy the need to hide in dark secluded places (different types of nest boxes) and one which could satisfy the need to make sleeping nests (different types of nesting materials). The study in Chapter 5 revealed that the preference of male and female mice for nesting materials was much stronger than for nest boxes. The mice even accepted a (previously avoided) grid floor to have access to the nesting material. The fact that the animals are able to manipulate the materials, thus controlling several aspects of their environment, might be an important motivation for the preference for this type of enrichment.

Enrichment may influence brain anatomy, behaviour and physiological systems of the body (see references in Introduction). Behavioural changes may even be so obvious that in a ‘blind’ experiment, human observers were able to identify the previous housing conditions (either standard or enriched) by only observing the behaviour of rats in a neutral environment (Renner & Hackett Renner 1993). Results of the studies described in this thesis indicate that the degree of complexity of the enrichment plays a role in the level of the behavioural and physiological effects. Cages enriched with a combination of nesting material, a climbing grid and a nest box changed the time budgets of mice, as well as their behaviour in an open field test, hole board test and cage emergence test (Chapters 2, 7 and 8). But when the preferred nesting material was provided as the only cage enrichment, no significant effects on the behaviour of mice in an open field test or aluminium foil test, nor influences on several physiological variables were found (Chapter 6). Several possible causes for enrichment effects have been described (see overview by Van Rijzingen 1995). The combination of physical, auditory, olfactory, tactile, visual and/or social stimuli, rather than a single factor seems to be important in generating an enrichment effect.

For generations, laboratory mice have bred equally well with and without nesting material (Van Oortmerssen 1971). Therefore one might say that nesting material is not essential for survival and reproduction. But it certainly adds
something to their specific needs, because they are strongly motivated to use it. For that reason, nesting material should be considered as enrichment. Nesting material is a general applicable enrichment for all mice, not only for females in breeding facilities. Furthermore, it can be provided to groups of mice but also to individually housed mice, which do not have the companionship of cage mates to huddle with for warmth and shelter. The long-term provision of (preferred) nesting material showed no major effects on the physiology or behaviour of the mice (Chapter 6). In view of the fact that the animals preferred nesting materials in preference tests and were also highly motivated to gain access to nesting materials, there seems to be no good reason to deprive laboratory mice from this form of enrichment.

Besides consequences for the animals, implementation of an enrichment programme may also have consequences for animal husbandry. In certain enriched housing systems the animals are more difficult to monitor, e.g. because they can hide in the shelters or nesting material which are provided. It is also possible that it is more difficult to remove the animals from their cages, because they have more space for fleeing or they have shelters or climbing facilities to take refuge in. It may cause severe stress if the animals have to be chased for this purpose, which might counteract positive effects of enrichment. In the study described in Chapter 6 the effects of enrichment on the behavioural response to handling was studied. It was expected that enriched housed animals were easier to handle because they were more tranquil, but the results were inconclusive.

Handling and management effects may differ between species. Gerbils raised in environments provided with a shelter were more difficult to capture and restrain and were more aggressive towards the experimenter than gerbils from standard laboratory environments (Clark & Galef 1980). On the other hand, studies on rabbits in group housing systems revealed that, although the animals in general flee to a hiding place, this facilitates their capture (Love 1994; Whary et al 1993). Enriched environments may give animals a more secure feeling, because they have more control over their environments, e.g. they can avoid or flee from frightening stimuli.

Enrichment should not only be stimulating for the animals, but it must also be manageable. This means that the enrichment must be easy to implement, to remove, clean, and replace. This is important for the workload of the personnel, and for their motivation and willingness to work with and to improve the enrichment programme (Van de Weerd & Baumann 1995). When including the design, maintenance and evaluation of enrichment programmes into the formal job responsibilities of animal care staff it may generate greater motivation and job satisfaction and a greater bond between caretakers and their animals (Benn 1995;

Although environmental enrichment might be of benefit for the animals, introducing an enrichment programme may jeopardise the standardisation of experiments. Standardisation of animal experimentation can be described as defining the properties of the animal (or animal population) and its environment, and the subsequent keeping constant or regulating (controlled varying) of these properties (Beynen et al 1993). The consequence is, that the response of the animals to treatment is as standardised as possible and the reproducibility of group mean results from one experiment to another is increased. The comparability of results within and between laboratories is also improved by standardisation (Beynen et al 1993; Clough 1987). The genetic background of experimental animals is in general standardised by selective breeding programmes. Genetic uniformity of the animals, however, does not mean that the animals will be phenotypically identical. Their response to experimental procedures can still vary, because this is only one of the factors influencing measured values. Other sources of variation are the pre- and postnatal environment and so-called intangible variance (Beynen et al 1993; Gärtner 1990; Van Zutphen et al 1993).

Environmental standardisation is not achieved when laboratories all develop their own individual strategies of enrichment. Comparison of results from different laboratories may be difficult if for example, one laboratory provides large enriched cages for groups of animals while another provides only one enrichment object to individually housed animals. Enrichment in itself can easily be standardised. The composition of nesting material for example, the amounts provided, the rate of replacement and hygiene (most materials can be autoclaved or sterilised) can all be well-defined.

Enrichment should not be a process of randomly applying objects which seem attractive for animals, but it should be a well designed and critically evaluated programme with well defined objectives. Care should be taken that enrichment strategies are implemented from the perspective of an animal, considering animal demands, and not only for the benefits of the caretakers (Newberry 1995; Rose 1994; Stauffacher 1994).

The introduction of enrichment may change certain characteristics of animals, and as a consequence, experimental results may not be comparable with previously found results. This, however should not hamper the introduction of enrichment, as it may be questioned whether the maintenance of animals in unresponsive environments makes them adequate models for extrapolating results to humans (Markowitz & Gavazzi 1995). Animals in an enriched environment are more competent to control their environment and therefore learn
to cope with novel and unexpected changes, as they are better adapted to their environment (Chamove 1989a; Rose 1994; Wemelsfelder 1994). Animals from standard housing conditions when brought into experimental situations are expected to react with more fear and stress than ‘enriched’ counterparts, which are more used to stimuli due to enrichment and habituate faster to new circumstances. In this way, more variation in reaction to novelty can be expected from animals from standard housing conditions in comparison with animals from enriched conditions. The results of experiments with enriched housed animals may therefore show less variation. Several authors have stated that animals from enriched housing conditions are physiologically and psychologically more stable and are therefore considered as more refined animal models, which ensure better scientific results (Bayne 1996; Benn 1995; Rose 1994; Spinelli & Markowitz 1985). Eventually the use of ‘enriched’ animals might lead to a reduction in the number of animals necessary for obtaining valid experimental results.