

Expert Commentary

**HOUSING INFLUENCES RESEARCH RESULTS AND
ANIMAL WELFARE IN GOLDEN HAMSTERS
(*MESOCRICETUS AURATUS*): THE INFLUENCE OF SIZE
AND STRUCTURE OF SHELTERS ON THE BEHAVIOUR**

***Esther Gerber, Sabine G. Gebhardt-Henrich*¹, Evelyne M.
Vonlanthen, Katerina Fischer, Andrina R. Hauzenberger
and Andreas Steiger***

University of Bern
Vetsuisse Faculty, Division of Animal Housing and Welfare,
Bremgartenstrasse 109a, CH-3012 Bern, Switzerland

ABSTRACT

Since 80 years golden hamsters have been kept as laboratory animals and pets in large numbers; captive hamsters now outnumber wild conspecifics. In our experimental studies we addressed the following aspects of housing and how they could influence research with golden hamsters and the welfare of laboratory and pet hamsters. 1. Thirty female golden hamsters (*Mesocricetus auratus*) were provided with three different shelter types (small, large undivided and large divided) and were observed for their favoured sleeping place and where they placed food, urine and faeces. In addition, their tunnel building was registered. Once a week for five weeks, each shelter and cage was examined and cleaned afterwards. The hamsters slept inside the shelter without exception. Hamsters in all three groups preferred to sleep in areas away from the entrance hole and animals with large divided shelters avoided the front compartment. Shelters were also used frequently for food storing and urination. Hamsters in small shelters urinated significantly

* Contact for correspondence and requests for reprints: sabine.gebhardt@bvet.admin.ch
Centre for proper housing of poultry and rabbits (ZTHZ) Federal Veterinary Office FVOBurgerweg 22, CH-3052
Zollikofen Switzerland

Tel.: +41 (0)31 915 3513 Fax: +41 (0)31 915 3514

¹ Present address: Centre for proper housing of poultry and rabbits (ZTHZ), Federal veterinary office FVO,
Burgerweg 22, CH-3052 Zollikofen, Switzerland.

more often additionally or exclusively outside the shelter than those in large divided shelters. Food and urine at the same place was found most often in large divided shelters. In comparison with the large undivided shelters, the hamsters with large divided shelters built fewer and shorter tunnel systems. This study demonstrates that golden hamsters use the shelter, whatever structure it has, above all for sleeping, but also for urinating and food storing. This experiment contradicts the expectation that hamsters, which have a shelter with two compartments, may separate the places for sleeping, urinating and hoarding their food. 2. *Running wheel*: Female golden hamsters were kept with large functional or non functional running wheels and their behaviour and lifetime reproductive success was examined. Females with functional wheels had significantly larger litters and showed significantly less stereotypical wire-gnawing than females with non-functional wheels. 3. *Cage size*: Female hamsters were kept in four different cage sizes (1800 cm² up to 10000 cm²). Those in the small cages gnawed significantly longer and more frequently at the wire than females in larger cages. 4. *Depth of bedding*: Male golden hamsters were kept in cages with 80, 40, or 10 cm deep wood shavings. Hamsters kept with 10 cm deep bedding showed significantly more wire-gnawing than those kept in deep bedding and bedding depth influenced the circadian rhythm. Our studies show that various aspects of housing can influence the behaviour of golden hamsters with implications on research and welfare.

Keywords: housing, golden hamster, animal welfare, behaviour, enrichment, shelter, tunnel.

INTRODUCTION

Golden hamsters (*Mesocricetus auratus*) are common laboratory animals and pets; captive hamsters now outnumber wild conspecifics (Gattermann, 2000). The natural habitat of the golden hamster is a fertile, agricultural and densely populated area in northern Syria, around the city of Aleppo. The hamsters live solitarily in subsoil burrow systems. Burrow depths were found to range from 36 to 106 cm, and their structure was simple, consisting of a single vertical entrance that proceeded to a nesting chamber and at least two tunnels divided from this chamber. A blind-ending tunnel was apparently used for urination. The remaining tunnels ran deeper at varying angles and were partially used for food storage. Faeces were found throughout the entire burrow. The mean length of the entire gallery system measured 200 cm and could extend up to 900 cm. Occupied burrows were plugged with a lump of earth. No general differences between female and male burrows were detected (Gattermann et al., 2001).

Housing conditions of hamsters as laboratory animals as well as popular pet animals differ from their natural habitat profoundly. Cage sizes are much smaller than natural territories. The closest distance between occupied hamster burrows was 118 m in Syria (Gattermann et al., 2001). Cage size and environmental enrichment affect the physiological and psychological well-being of captive rodents (see reviews by Russell, 2002; Sørensen et al., 2005; Balcombe, 2006 and references therein). Although poor housing has been known to distort research results (Würbel, 2001), little work has been done with the specific intent of improving the housing conditions of golden hamsters. Exceptions are the work by Kuhnen (1999), Bantin and Sanders (1989) on cage size, Mrosovsky et al. (1998) and Reeb and St-Onge (2005) on types of running wheels, Reeb and Maillet (2003) on environmental enrichment, and the review by Sørensen et al. (2005). As Reeb and Maillet (2003) pointed

out changes in housing conditions like larger cages and/or items of environmental enrichment might influence important research variables such as the circadian rhythm in golden hamsters. In this chapter we provide a short overview about our studies on aspects of housing in the golden hamster and present an investigation on three different shelter types and their usage by the hamsters in detail.

1. INFLUENCE OF A RUNNING WHEEL

A running wheel was the most valued enrichment item in a study of mice (Sherwin, 1998). In a study on the effect of a running wheel ten female golden hamsters were provided with a large running wheel (diameter: 30 cm) whereas ten females had an identically looking non-functional running wheel. All hamsters were kept singly in fairly large cages (5000 cm²) with wood shavings as bedding, a shelter, hay, and branches for gnawing. Their behaviour and lifetime reproductive success was examined. Females with functional wheels had significantly larger litters than females with non-functional wheels but the growth of their offspring did not differ. Females with wheels stopped running in the wheels when their young were less than 10 days old. The females with a functional wheel showed significantly less climbing and stereotypical wire-gnawing than females with non-functional wheels. Thus, the running wheel did not show any detrimental effects when hamsters were kept in large and enriched cages with ad libitum food and water. On the contrary, the well-being of hamsters with access to a running wheel seemed to be improved because they displayed less stereotypical wire gnawing (Gebhardt-Henrich et al., 2005). The effects of the running wheel on the behaviour were repeated in a study with male golden hamsters with the same results concerning the behaviour (P. Eberli, unpublished data).

2. CAGE SIZE

Similarly, cage size influenced stereotypic behaviour in female golden hamsters. Female hamsters were kept in four different cage sizes (1800 cm²= size of Macrolon IV, a common cage in laboratories, 2500 cm², 5000 cm², 10000 cm²). All hamsters were housed singly and there were fifteen hamsters per cage size. Enrichments included a shelter, hay, branches, and a running wheel. Those in the small cages gnawed significantly longer and more frequently at the wire than females in larger cages. However, stereotypic wire-gnawing was observed even in the largest cages (Fischer et al., 2007). Besides the frequency and duration of wire-gnawing no significant differences in the behaviour of hamsters in the different sized cages were found.

3. BEDDING DEPTH

Tunnel building is a natural behaviour of golden hamsters and it is also performed in captivity whenever possible (Kuhnen, 2002, Hauzenberger et al., 2006). In order to investigate the influence of bedding depth on the behaviour 45 male golden hamsters were

singly kept in cages with 80, 40, or 10 cm deep wood shavings (fifteen hamsters per treatment). All hamsters had a shelter, hay, branches, and a running wheel. All hamsters in 40 and 80 cm bedding constructed burrows which they occupied, none used the shelter for sleeping or food storing. Hamsters kept with 10 cm deep bedding showed significantly more wire-gnawing and a higher running wheel activity than the hamsters in the other groups. In 80 cm deep bedding wire-gnawing was never observed. Bedding depth influenced the circadian rhythm. The hamsters with medium or deep litter developed significant phase delays (Hauzenberger et al., 2006). Golden hamsters are an important laboratory animal in chronobiological research because they show a very stable circadian rhythm (Gattermann, 1984, Mrosovsky et al., 1989, Weinert et al., 2001). However, golden hamsters from one population in the wild displayed a strikingly different rhythm (Gattermann et al., 2008). Since circadian rhythms are largely influenced by environmental conditions the rhythms displayed in the laboratory might be artefacts due to the unnatural housing of the animals.

Providing deep bedding seemed the most important item to improve welfare because this aspect of housing alone prevented the occurrence of stereotypic wire-gnawing. However, hamsters in deep bedding accumulated more fat and the disturbance of the circadian rhythm might indicate a welfare problem.

In many instances it is not possible to provide hamsters with deep bedding due to space limitations or due to the necessity of frequent handling. Artificial shelters must substitute for the construction of burrows. The presence of dark shelters in particular proved to be decisive in reducing stereotypies in gerbils (Waiblinger, 2002, Wiedenmayer, 1997a,b). Without shelters and nesting material golden hamsters can be very aggressive and the aggressive behaviour decreases when shelters and nesting material are provided (Lochbrunner, 1956, McClure and Thomson, 1992). The Swiss Animal Protection recommends a shelter for hamsters, but does not specify how it should look like (Lerch-Leemann and Griffin, 1997). We are not aware of any study investigating the size or structure of the shelter and the usage by captive rodents. Shelters may differ profoundly from natural burrows, especially under laboratory conditions. The separation of urine and sleeping position might be important to avoid the irritating ammonia gas (Kuhnen, 1986).

In order to learn more about the hamster's preferences for the type of artificial shelters, we investigated the behaviour of female golden hamsters provided with shelters of three different sizes and structures. In particular, we wanted to examine whether the animals made use of two compartments to separate sleeping position and places for urination and food storing.

METHODS

Animals and Husbandry

All 30 female golden hamsters used in this study were bred at our facility. Two of the animals were progeny of the strain CrI: LVG (SYR) from Charles River, Germany. The remaining 28 hamsters belonged to the strain RjHan: AURA from Centre d'Élevage R. Janvier, France. Hamsters were kept in wire cages with plastic bottoms (95 x 45 x 57 cm including the wire top). Wood shavings (Allspan®, 10 cm deep) mixed with hay were

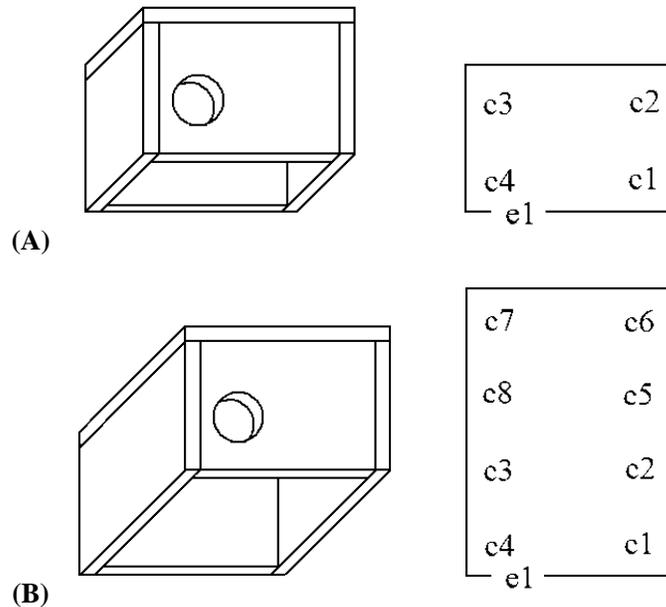
provided as bedding. Commercial hamster food (www.ericsschweizer.ch) and water were offered *ad libitum*. In addition, a small piece of fresh fruits or vegetables was given each day. During the experiment the hamsters were housed in a room with natural daylight from the top of the room. Temperature was unregulated, but well balanced over the different levels of the room and the experimental treatments. It ranged from 19 to 26°C (except once was measured 29°C) dependent on the outdoor temperature and increased steadily during the experiment. Humidity was also unregulated.

The animals were weaned between days 27 and 35 and within a litter randomly assigned to three experimental groups with different shelter types (small, large undivided, large divided), each group consisting of 10 animals. The two animals of the strain from Charles River were distributed in two different groups. The hamsters were placed singly in a cage as described above with a particular type of shelter. Before weaning, all had a shelter of the type ‘small’. Three to six weeks (balanced for treatments) to acclimatise were given before the start of the experiment.

The cages were put in a rack with four different levels, whereas the cages of one group were distributed on all different levels. The position of the cages stayed the same over the weeks of examination.

Material

All shelters were bottomless, made of fir wood and had a circular entrance of 5 cm in diameter on one side (Figure 1). They were positioned on the bedding surface. One group got a small shelter (SM: 20 x 14 x 14 cm), the second a large one (L1: 20 x 28 x 14 cm) and the third a large one, which was divided in the middle (L2: 20 x 28 x 14 cm). The wall, which divided the large shelter into two rooms, had a passage (5 cm in diameter) at the opposite side of the entrance (Figure 1).



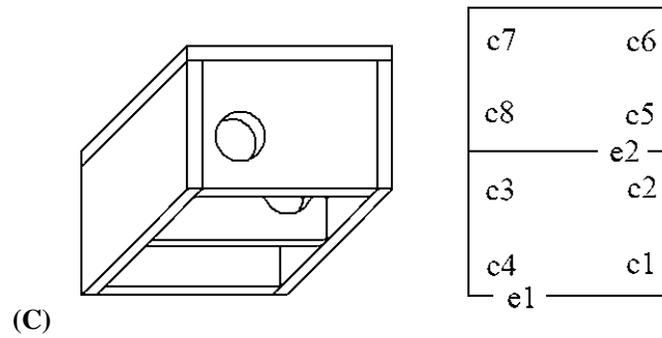


Figure 1 Shelter types. Three different shelter types were provided and the space inside was divided into four or eight imaginary areas (c1 – c4 / c8): (a) small, (b) large undivided and (c) large divided. The shelters had one entrance (e1) and the partition in large divided shelters had a hole (e2) opposite of the entrance.

Each cage was equipped with two cardboard tubes, a branch, a sand bath and a paper towel as nesting material. Figure 2 shows a clean cage.



Figure 2. A clean cage with an L2 shelter. The wire top is removed (a branch is missing because it was fixed at the wire top).

Procedure

The cage was examined every week during the sleeping period of the hamsters between the hours 8:00 am and 4:00 pm. For that, the cages were removed one after the other from the rack and the wire tops were removed. In each examination, first the shelter was lifted to locate the hamster. After that, the bedding was searched for urine, faeces, food and the paper towel.

The shelter was mapped into four (SM) or eight (L1, L2) imaginary areas named c1, c2 etc. (Figure 1). In addition, tunnel systems in the bedding were mapped. Tunnels were divided into four categories: no tunnel (score 0), short (up to 20 cm; score 1), medium long (21 – 40 cm; score 2) and long (41 cm and longer, score 3). Afterwards, the cage was cleaned by exchanging only the bedding in the shelter and in places where urine, faeces or food were found. The experiment lasted five weeks, therefore five examinations per animal were accomplished.

After the experiment all hamsters were given to private owners. The experiment was approved by the Cantonal Office of Agriculture (No 37/06).

Statistics

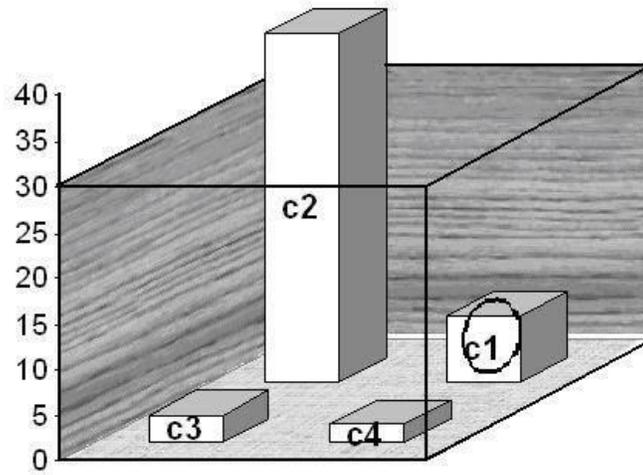
In order to obtain one measure for the sleeping position for each animal the most frequent location out of the five recorded locations per item was taken. In case there was no most frequent location this data point was considered missing. The data were analysed using the Kruskal-Wallis-test, except for the analysis of the frequency of the sleeping positions and urine deposition outside the shelter, for which Fisher's exact test was used. Results were considered statistically significant when $P < 0.05$. Analyses and plots were performed using NCSS and SAS.

RESULTS

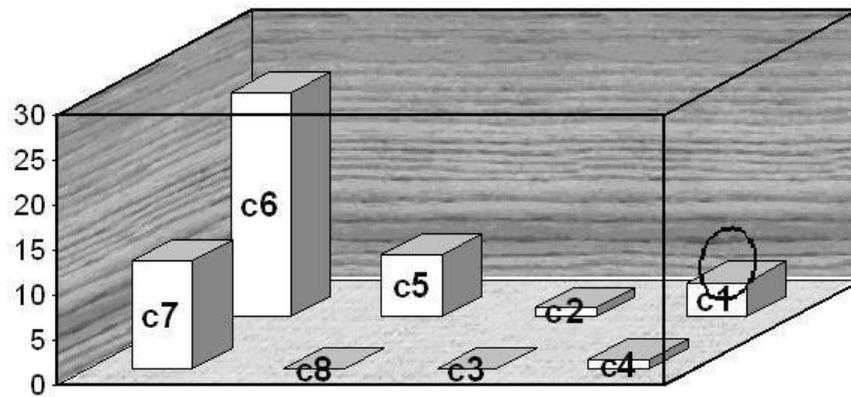
Sleeping Positions

All hamsters were found at the time of examination inside the shelter without exception. Some lay on the surface of the bedding, others were buried a few centimetres. Only four out of the 30 animals (13.3%) took the offered paper towel regularly (at least three times in five examinations) into the shelter and used it as nesting material. Seldom, the entrance of the shelter was plugged with bedding.

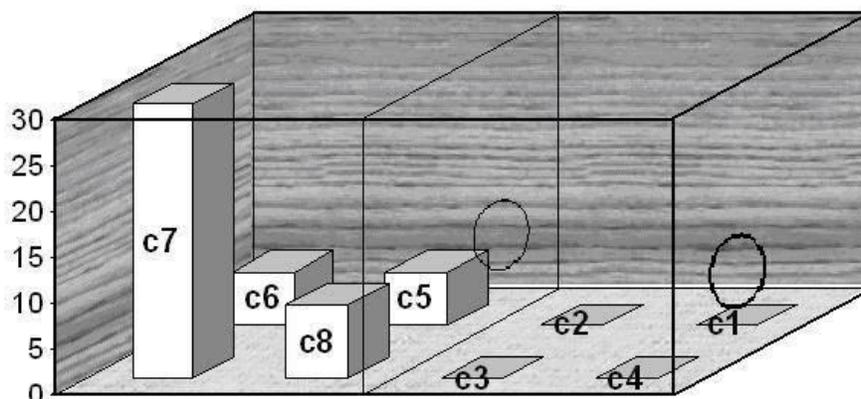
The sleeping positions are summarized in Figure 3.



(A)



(B)



(C)

Figure 3. Sleeping positions. Schematic representation of three shelter types with the entrance on the right side: (a) SM-shelter, (b) L1- and (c) L2-shelter. All sleeping positions recorded at five observations which were at weekly intervals are summarized for each area (c1 – c4 / c8) inside the shelters (n = 10 for each group).

The places where the hamsters were found most often in each group (SM: c2, L1: c7, L2: c6) have in common that they were situated diagonal of the entrance of the room. No hamster was ever found in the front room (c1 – c4) in the L2 group. When the positions of the small shelters were recoded as the corresponding areas in the large shelters (c2 => c6, c3 => c7) the positions between the treatments were significantly different (Table 1, $\chi^2_6 = 23.0$, $P < 0.0001$). In detail, the sleeping position of the L2 group was significantly different to that of the SM group ($\chi^2_3 = 20.0$, $P < 0.0001$) and the L1 group ($\chi^2_2 = 11.4$, $P = 0.004$), but there was no significant difference between groups SM and L1.

Table 1. Sleeping positions of golden hamsters with different shelters

		c1	c5	c6	c7	sum
SM	frequency	1	0	9	0	10
	percentage	10	0	90	0	100
L1	frequency	0	0	6	2	8
	percentage	0	0	75	25	100
L2	frequency	0	1	0	9	10
	percentage	0	10	0	90	100

The most registered position of each hamster during the five weeks was used. The areas of the small shelters were recoded (c2 = c6; c3 = c7) in order to compare all three treatments. Two animals did not have a commonest position and are missing.

The selection of a sleeping position was compared with the choice in the following week. Only two hamsters were observed in a different position every week (four times). Both lived in L1 shelters. Animals in the SM group were found in changed sleeping places 1.2 times on

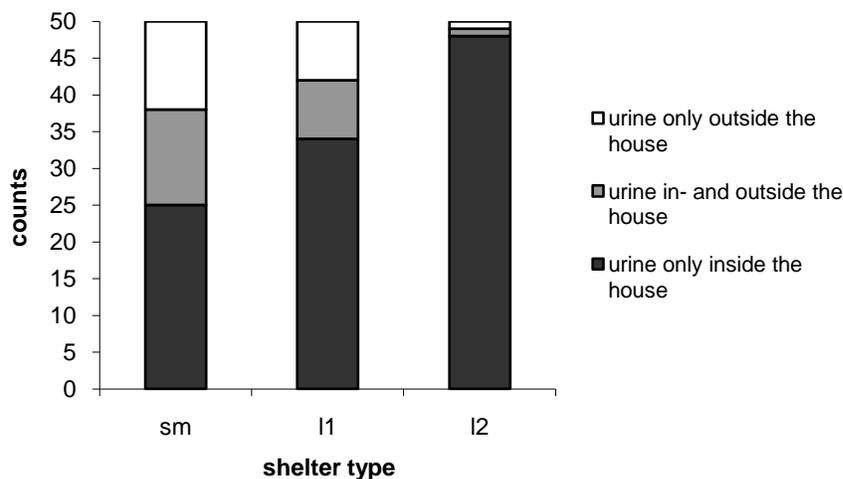
average, those with L1 and L2 shelters 2.3 and 2.2 times, respectively. In large shelters (L1 and L2), hamsters were registered in varied position significantly more often than animals in SM shelters ($\chi^2_1 = 4.93$, $P: 0.026$).

Urine and Food

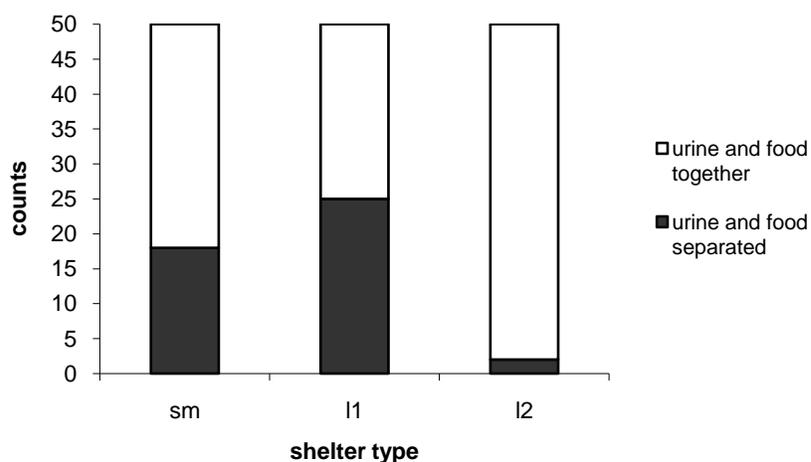
Urine was found for the most part inside the shelters (Figure 4a), often distributed in more than one places (up to seven places; average: 2.4). In some cages, one (usually) to three (rarely) additional places to urinate outside the shelter were identified. Ten hamsters urinated regularly (at least three times in five examinations) outside the shelter, regardless of whether there was urine in the shelter or not. Six of them belonged to the SM group, four to the L1 group and none to the L2 group. These differences were statistically significant ($\chi^2_2 = 8.4$, $P: 0.01$). In only three animals (two of the SM, one of the L1 group) the shelter was registered free of urine in most examinations, that means at least in three of five.

In a total of 150 data records only in five (3.3%) no food storage was found. The food was always put inside the shelter with just one exception. Inside the shelter, hamsters distributed the food in two different corners on average (maximum five). Few animals hoarded food in places outside the shelter at the same time, but no member of the L2 group was registered among them (SM: 12%; L1: 14%; L2: 0%).

Additionally, it was determined, whether the animals urinated in the places, where they slept or stored food. Hamster and urine were found in the same place in 18% (L1 group) to 34% (L2 group) and there was no significant difference among the groups. However, animals with L2 shelters placed urine and food significantly more often in the same spot (96%) than residents of an L1 (50%) and an SM (64%) shelter ($\chi^2_2 = 16.34$, $P: 0.0003$, $N = 30$; Figure 4b).



(A)



(B)

Figure 4. Urine positions and their connection with food storing. The location of urine (a) and its relation to food storing (b) found at five observations, each one week after previous cage cleaning for hamsters provided with three different shelter types ($n = 10$ for each group)

In all groups faeces were found all over the shelter and also at different sites outside the shelter.

Tunnel Building

Each week, tunnels were mapped and destroyed afterwards while the bedding was partially exchanged, thus the hamsters had to rebuild them. Most registered tunnels started in a corner of the shelter (67%) and ended blindly somewhere in the cage. In a little less than half of the burrows (47%) there was urine at the end. Food was placed in one fourth (25%) of the tunnels, sometimes alone (45%) and sometimes together with urine (55%).

In 15 of 30 animals there was never any tunnel detected after cleaning the bedding one week before (Figure 5). Six among them belonged to the SM group, two lived in an L1 and seven in an L2 shelter. In the cages of five animals, tunnels were found regularly (at least three times in five examinations). Two of them were members of the SM, three of the L1 group. Analysis of the mean of the tunnel scores revealed, that it was significantly lower in the L2 group compared with the L1 group ($\chi^2_1 = 4.8, P = 0.03$).

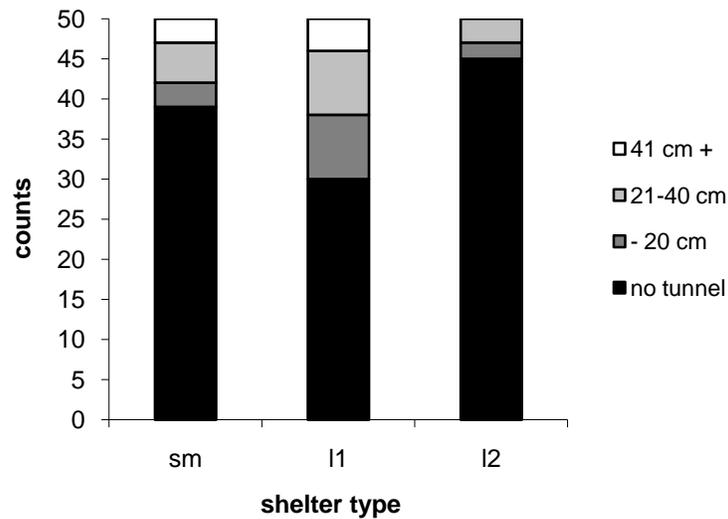


Figure 5 Tunnel building. Tunnel building found at five observations, each one week after cage cleaning for hamsters provided with three different shelter types. If a tunnel existed, its length was divided into three groups: 20 cm and shorter, 21 to 40 cm or longer than 40 cm ($n = 10$ for each group).

DISCUSSION

Hamsters used the shelter without exception. In the wild, living in burrows offers a relatively stable ambient temperature and humidity to the inhabitants and protects against predation (Kuhnen, 1986). Obviously, the need to retreat persists under laboratory conditions. Hauzenberger et al (2006) found that golden hamsters in deep bedding (40 and 80 cm) used an artificial shelter only as an occasional cover. Therefore, it may not be necessary to provide a shelter when there is enough bedding to dig tunnels. However, when this possibility does not exist, this study leads to the recommendation to offer a shelter.

In general, in every shelter type the most preferred sleeping corner was the one diagonally from the hole (entrance in SM and L1 shelters and passage between the two rooms in L2 shelters). We suggest that the hamsters chose this place because it was the most hidden and little light reached them during sleeping hours. This result is confirmed by the observation that every animal of the L2 group always slept in the back room. Several burrow-dwelling rodents, including hamsters, were found to prefer dark areas (Warden and Sachs, 1974; Pratt and Goldman, 1986; van den Broek et al., 1995; Würbel et al., 1998). Waiblinger and König (2004) illustrated the importance of a dark retreating possibility in gerbils by showing that gerbils reared with access to an opaque artificial burrow developed less stereotypic digging than those reared in transparent artificial burrows.

In all three groups we found animals of the SM group least often in a changed sleeping place compared with the previous week. These hamsters had just four positions to choose, whereas the animals of the other groups had eight. Nevertheless, this does not explain the difference compared to the animals of the L2 group, since they never used the front room and

consequently also changed between four corners. However, in SM shelters the best-hidden place was obviously c2, while the back room of L2 shelters was generally dark and therefore the difference between the areas was smaller than in SM shelters.

Hamsters of the SM group were noticed to urinate most frequently outside the shelter. Probably, this was simply because they had less space in the shelter.

All hamsters usually stored food inside their shelter. Hamsters need to eat small meals at regular two-hour intervals. Therefore, the food caches serve not only as an emergency store, but hamsters also eat from them during daytime (Toates, 1978). In addition to a tunnel for urination, wild hamsters build one or more tunnels and store food in there (Gattermann et al., 2001). However, the hamsters in our study often put urine and food in the same places. In particular, animals living in L2 shelters did not use the two rooms to separate urine and food. Contrary to our expectation, we found urine of these animals even more frequently together with food. The fact that they grew up in a small shelter without division may have influenced this behaviour. Possibly, they did not change a habit, which they learnt in early days. Therefore, it would be interesting to repeat the experiments with animals, which were already born in different shelter types.

Several of our findings indicate that hamsters in large structured shelters build less extensive tunnels than animals with large unstructured shelters: 1. The tunnel score of the L2 group was significantly lower than that of the L1 group. 2. We registered no hamster with an L2 shelter building tunnels regularly, but three of the L1 group doing this. 3. Lack of a tunnel in all five examinations occurred more often animals of the L2 group (seven), than in the L1 group (two). 4. All tunnels found in animals with an L2 shelter were shorter than 40 cm, in contrast to these in L1 shelters. Therefore, we suppose that shelter type and digging behaviour are connected. Wiedenmayer (1997a) suggested that stereotypic digging develops in housing conditions in which young gerbils cannot achieve their essential goal, i.e. cannot retreat into a dark space. In our study, the back room of the L2 shelters was obviously darker than the room of L1 shelters. This may be a reason why we found more tunnel building in hamsters of the L1 group and if so, it indicates that also in golden hamsters digging behaviour is more goal oriented than activity oriented. To prove that a suitable shelter reduces stereotypic behaviour in golden hamsters requires further examinations.

Although hamsters in large divided shelters built tunnels least frequently, a majority (60% and 78%) of the L1 and SM group did not build burrows either. The unnatural bedding and the limited digging depth may have influenced the digging behaviour. Besides, sometimes it was difficult to determine the tunnels clearly, because the bedding did not allow building very stable burrows. Anyway, the level of inaccuracy was the same in all three groups.

CONCLUSION

This study shows that female hamsters used a shelter, independent of its size and structure. They frequently used it for urinating or food storing, and always for sleeping. Therefore, a shelter should always be provided, except when deep bedding is available. Golden hamsters prefer to sleep in well hidden and dark places. This needs to be considered when choosing a shelter.

In general, various aspects of housing like cage size and items of enrichment (running wheel, depth of bedding, size, and structure of shelter) significantly influenced the behaviour of golden hamsters. Among the affected behavioural elements were often studied variables like stereotypic behaviour and circadian rhythms. Therefore, housing conditions are decisive for the interpretation of research results firstly because they directly influence the outcome and secondly because they affect the well-being of the laboratory animals (indicated by the level of stereotypic behaviour). Well-being of laboratory animals might indirectly influence research results in various ways. Research results from studies using unnatural housing conditions might yield artefacts compared with the natural behaviour of the animals as shown by Gattermann et al. (2008).

ACKNOWLEDGEMENTS

Special thanks to P. Eberli and A.R. Hauzenberger for helping take care of the hamsters and to A. Gerber for constructing the shelters. Carla Holmes helped with the language.

REFERENCES

- Balcombe, J. P. (2006). Laboratory environments and rodents' behavioural needs: a review. *Laboratory Animals* 40: 217 - 235.
- Bantin, G. C. & Sanders, P. D. (1989). Animal caging: is big necessary better? *Animal Technology* 40: 45 - 54.
- Fischer, K., Gebhardt-Henrich, S. G. & Steiger, A. (2007). Behaviour of golden hamsters (*Mesocricetus auratus*) kept in four different cage sizes. *Animal Welfare* 16: 87-95.
- Gattermann, R. (1984). Zur Biorhythmik des Goldhamsters (*Mesocricetus auratus* WATERHOUSE 1839) I. Zirkadiane Rhythmen. *Zool. Jb. Physiol.* 88: 471 - 489.
- Gattermann, R. (2000). 70 Jahre Goldhamster in menschlicher Obhut - wie gross sind die Unterschiede zu seinen wildlebenden Verwandten? *Tierlaboratorium* 23: 86 - 99.
- Gattermann, R., Fritzsche, P., Neumann, K., Al-Hussein, I., Kayser, A., Abiad, M. & Yakti, R. (2001). Notes on the current distribution and the ecology of wild golden hamsters (*Mesocricetus auratus*). *J. Zool. Lond.* 254: 359 - 365.
- Gattermann, R., Johnston, R. E., Yigit, N., Fritzsche, P., Larimer, S., Ozkurt, S., Neumann, K., Song, Z., Colak, E., Johnston, J. & McPhee, M. E. (2008). Golden hamsters are nocturnal in captivity but diurnal in nature. *Biology letters* 4: 253-255.
- Gebhardt-Henrich, S. G., Vonlanthen, E. M. & Steiger, A. (2005). How does the running wheel affect the behaviour and reproduction of golden hamsters kept as pets? *Applied Animal Behaviour Science* 95: 199 - 203.
- Hauzenberger, A., Gebhardt-Henrich, S. G. & Steiger, A. (2006). The Influence of Bedding Depth on Behaviour in Golden Hamsters (*Mesocricetus auratus*). *Applied Animal Behaviour Science* 100: 280 - 294.
- Kuhnen, G. (1986). O₂ and CO₂ Concentrations in burrows of euthermic and hibernating golden hamsters. *Comparative Biochemistry and Physiology* 84A: 517 - 522.

- Kuhnen, G. (1999). The effect of cage size and enrichment on core temperature and febrile response of the golden hamster. *Laboratory animals* 33: 221-227.
- Kuhnen, G. Comfortable Quarters for Hamsters in Research Institutions. In: Reinhardt, editor. *Comfortable Quarters for Laboratory Animals*. Washington, DC 20007: Animal Welfare Institute; 2002; 33 - 37.
- Lerch-Leemann, C. & Griffin, A. 1997 Hamster (Goldhamster und Zwerghamster) Schweizer Tierschutz STS.
- Lochbrunner, A. (1956). Beiträge zur Biologie des Syrischen Goldhamsters (*Mesocricetus auratus*) (Nehring). *Zoologische Jahrbücher Physiologie* 66: 389 - 428.
- McClure, D. E. & Thomson, J. L. (1992). Cage Enrichment for Hamsters housed in Suspended Wire Cages. *Contemporary Topics* 31: 33.
- Mrosovsky, N., Salmon, P. A. & Vrang, N. (1998). Revolutionary Science: an improved running wheel for hamsters. *Chronobiology International* 15: 147 - 158.
- Mrosovsky, N., Reeb, S. G., Honrado, G. I. & Salmon, P. A. (1989). Behavioural entrainment of circadian rhythms. *Experientia* 45: 696 - 702.
- Pratt, B. L. & Goldman, B. D. (1986). Activity rhythms and photoperiodism of Syrian hamsters in a simulated burrow system. *Physiology & Behavior* 36: 83 - 89.
- Reeb, S. G. & Mailliet, D. (2003). Effect of cage enrichment on the daily use of running wheels by Syrian hamsters. *Chronobiology International* 20: 145 - 156.
- Reeb, S. G. & St-Onge, P. (2005). Running wheel choice by Syrian hamsters. *Laboratory animals* 39: 442-51.
- Russell, W. M. S. The Ill-Effects of Uncomfortable Quarters. In: Reinhardt, editor. *Comfortable Quarters for Laboratory Animals*. Washington, DC 20007: Animal Welfare Institute; 2002; 1 - 5.
- Sherwin, C. M. (1998). The use and perceived importance of three resources which provide caged laboratory mice the opportunity for extended locomotion. *Applied Animal Behaviour Science* 55: 353 - 367.
- Sørensen, D. B., Krohn, T., Hansen, H. N., Ottesen, J. L. & Hansen, A. K. (2005). An ethological approach to housing requirements of golden hamsters, Mongolian gerbils and fat sand rats in the laboratory - A review. *Applied Animal Behaviour Science* 94: 181 - 195.
- Toates, F. (1978). A circadian rhythm of hoarding in the hamster. *Animal Behaviour* 26: 630-631.
- van den Broek, F. A. R., Klompaker, H., Bakker, R. & Beynen, A. C. (1995). Gerbils prefer partially darkened cages. *Animal Welfare* 4: 119 - 123.
- Waiblinger, E. Comfortable Quarters for Gerbils in Research Institutions. In: Reinhardt, editor. *Comfortable Quarters for Laboratory Animals*. Washington, DC 20007: Animal Welfare Institute; 2002; 18 - 25.
- Waiblinger, E. & König, B. (2004). Refinement of gerbil housing and husbandry in the laboratory. *Animal Welfare* 13: 229-235.
- Warden, A. W. & Sachs, B. D. (1974). Circadian rhythms of self-selected lighting in hamsters. *Journal of Comparative Physiology* 91: 127 - 134.
- Weinert, D., Fritzsche, P. & Gattermann, R. (2001). Activity rhythms of wild and laboratory golden hamsters (*Mesocricetus auratus*) under entrained and free-running conditions. *Chronobiology International* 18: 921 - 932.

- Wiedenmayer, C. (1997). Causation of the ontogenetic development of stereotypic digging in gerbils. *Anim. Behav.* 53: 461 - 470.
- Wiedenmayer, C. (1997). Stereotypies resulting from a deviation in the ontogenetic development of gerbils. *Behavioural Processes* 39: 215 - 221.
- Würbel, H. (2001). Ideal homes? Housing effects on rodent brain and behaviour. *TRENDS in Neurosciences* 24: 207 - 211.
- Würbel, H., Chapman, R. & Craig, R. (1998). Effect of feed and environmental enrichment on development of stereotypic wire-gnawing in laboratory mice. *Appl. Anim. Behav. Sci.* 60: 69 - 81.