Running wheel choice by Syrian hamsters

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Summary

The present study investigated the preference of male and female Syrian hamsters, *Mesocricetus auratus*, for different types of running wheels. Hamsters were placed individually in sets of multiple cages linked by tunnels, each cage with a different running wheel. The number of wheel revolutions in each cage was tallied daily over 40 days. The hamsters did not express a preference when offered a choice of a running surface made of metal rods spaced 9 mm apart and a similar running surface covered in plastic mesh to prevent the possible slippage of feet between the rods. The hamsters did express a clear preference for larger wheels (35 versus 23 cm diameter), and for completely circular wheels over truncated ones. They neither favoured nor rejected wheels with small obstacles along the running surface. In all experiments, preferences were more strongly expressed by males than by females. Running wheels for hamsters may be improved by enlarging their diameter (to the standards often used for rats, if practically possible) and by ensuring good footing on the running surface (a space no larger than 9 mm between evenly spaced rods seems sufficient to achieve this, at least in large wheels and for hamsters older than 55 days). Installing obstacles along the running surface does not appear to make the wheel more interesting to hamsters.

Keywords Syrian hamster; golden hamster; running wheel; choice; preference; animal welfare

Hamsters are fairly common subjects of study in biomedical research, yet little work has been done with the specific intent of improving their captivity conditions. Exceptions include Arnold and Estep (1994) on cage floor choice, Mrosovsky *et al*. (1998) on running wheel choice, Kuhnen (1999) on cage size, and Reebs and Maillet (2003) on environmental enrichment. In the case of Mrosovsky *et al*. (1998), Syrian hamsters (*Mesocricetus auratus*) had constant access to running wheels, and it was noted that small skin lesions occasionally appeared on the side of the animals' hind legs. Mrosovsky and his co-workers suspected that the lesions developed as a result of the legs sometimes slipping between the rods that formed the running surface of the wheels. They therefore sought to improve the wheel by wrapping it in a plastic mesh to make the running surface more solid. Their study showed that hamsters preferred these improved wheels in choice tests, ran more in the improved wheels than they did in normal ones, and stopped developing skin lesions.

Mrosovsky *et al*. (1998) worked with wheels (RC Hagen, distributors) that were 17.5 cm in diameter, with the running surface being made of transverse rods 7.5 cm long and 1.6 mm thick, spaced 12 mm apart. In our laboratory, hamsters have access to wheels (Nalgene, F-size for rats) that are 35 cm in diameter, with rods 9.5 cm long and 2 mm thick, spaced 9 mm apart (actual open space between rods: 7 mm). Probably because of those different dimensions, most notably the smaller interval between rods, our

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hamsters do not develop skin lesions and their legs have not been observed slipping between rods. We were nevertheless curious to see whether hamsters would still prefer a more solid running surface. We therefore offered Syrian hamsters a choice between our wheels with and without a plastic mesh around them. Our 'with mesh' category was further divided into two groups: one for which the mesh was wrapped around the outside of the wheel (as Mrosovsky and co-workers had done) and the other for which the mesh was laid on the inside of the wheel. Furthermore, we tested both male and female hamsters, as opposed to males only in Mrosovsky *et al*. (1998).

Mrosovsky *et al*. (1998) also offered male hamsters a choice between a small diameter wheel (13 cm) and a larger one (17.5 cm). The larger wheel was clearly preferred. We asked whether a similar preference would extend to our even larger wheels, for males as well as females. We offered Syrian hamsters a choice between Nalgene's F-size wheels for rats (35 cm diameter) and Nalgene's L-size wheels for mice (23 cm diameter).

Finally, inspired by reports that mice, *Peromyscus* spp., can develop a taste for square wheels or wheels with obstacles along the running surface (Kavanau & Brant 1965, Kavanau 1966, 1967), we offered male and female hamsters a choice between wheels that were conventionally circular versus others with irregularities such as platforms and 'speed bumps'.

Plastic mesh experiment

Material and methods

This and subsequent experiments were all conducted under approval by the Université de Moncton's Animal Care Committee (protocol No. 02-10).

Ten male hamsters (Lak:LVG[SYR]BR), 48–55 days old, were obtained from Charles River Canada. Upon arrival in the laboratory, each hamster was placed in its own three-cage system. Such a system consisted of three polypropylene cages ($47 \times 26 \times 20$ cm each, F-size cage, Nalgene) placed side by side and linked by tunnels (Habitrail, Hagen). The tunnel arrangement was a line 67 cm long with three descending embranchments, one at each end and one in the middle of the line. Each descending section, 15 cm long, gave access to a separate cage. This system allowed hamsters to enter any cage from any other cage. Litter (heat-treated hardwood chips, 'Beta-Chips', Northeaster Products, 1 L per cage) and food pellets for laboratory rodents (Hagen) were present in each cage. A water bottle was attached to one of the end cages in the linear arrangement.

Each of the three cages had a Nalgene F-size wheel (see Introduction for dimensions). One wheel was unmodified (no mesh = NM). Another wheel had a strip of mesh tightly wrapped around it (external mesh = EM), while the last wheel had a strip of mesh pushed against it from the inside (internal mesh = IM). The mesh (Vexar Inc) had ribs of 1.2 mm forming openings of 4×4 mm. The order in which the three types of wheel occurred along the three-cage arrangement was systematically varied from hamster to hamster (so that each wheel type occupied the same cage position approximately the same number of times) to minimize the effect of any bias that could occur from the fact that hamsters like to nest in end cages (Reebs & Maillet 2003) and that only one of the three cages had a water bottle. A small-gauge electronic wire was used to secure the mesh in evenly distributed places along the running surface.

Each wheel was connected to a micro-switch. Wheel revolutions were tallied by computer (Dataquest III software). The first two days were ignored (i.e. considered as a period of exploration for the hamsters, though it must be said that hamsters invariably start using tunnels within a few hours of arrival in the laboratory) and the next 20 days were used to determine which wheel was used most by each hamster. (We first analysed the data in five-day blocks, but no consistent pattern of change from block to block emerged, and therefore we present the results of all 20 days considered as one block.) Then, the favourite wheel of each subject was locked (here the favourite wheel was determined based on the average number of daily revolutions over the last five days). The day that immediately followed the locking was ignored, and the next 10 days were used to determine preference between the two remaining wheels. Then the locked wheel was unlocked, the next day disregarded, and the final 10 days of the experiment were used to determine whether the old preference returned.

Hamsters commonly pile up part of their bedding material to make a nest on which they sleep. The position of the hamsters and their nest was noted daily, during the light period. A note was also made daily of the presence or absence of faeces in each cage. Litter was changed at 10-day intervals. The weight of each hamster was noted at the beginning and end of the experiment, and at each litter change. Food and water were changed or added as needed. The photoperiod was 14:10 h light:dark, provided by incandescent lights. Temperature was $21 \pm 1°C$.

At the end of this experiment, the equipment was thoroughly washed, and the experiment was repeated with 10 females, 48–55 days old, also obtained from Charles River Canada.

Statistical analysis was done with SPSS for Windows. One type of analysis consisted of comparing the average number of daily revolutions in each wheel type. Another consisted of assigning preference ranks to each wheel for each hamster (rank No. 1 being the wheel with the most daily revolutions on average). Significance level was set at $P = 0.05$. In the text, means are accompanied by standard deviations.

Results

The hamsters visited all three cages every night, as evidenced by the presence of faeces in all cages and by the recording of at least some wheel revolutions in all wheels on any single night.

Figure 1 shows the mean number of daily revolutions in each wheel type by each individual hamster during the 20 days that preceded the wheel block. Some hamsters developed a clear preference for a particular wheel type, though not necessarily the same

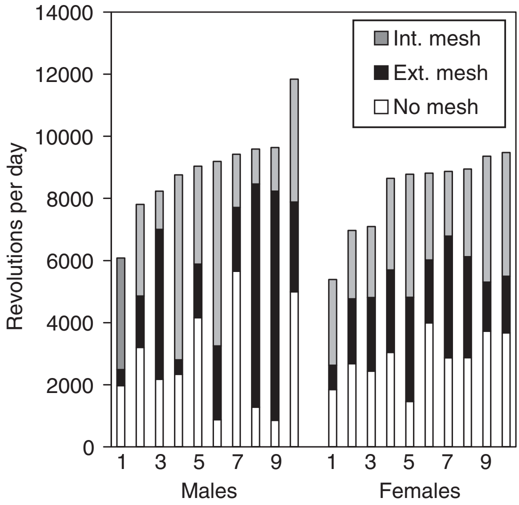

Figure 1 Number of daily wheel revolutions, averaged over 20 days, by individual male and female Syrian hamsters that had simultaneous access to three running wheels: one with a running surface made of evenly spaced rods 9 mm apart (no mesh), one with the same surface covered with a plastic mesh on the inside (int. mesh), and one with mesh on the outside (ext. mesh)

one (e.g. males Nos 6, 7, 8, 9), while others used all wheel types fairly evenly (e.g. males Nos 2, 10; females Nos 2, 3, 4, 7, 8).

No significant difference was detected in the average number of revolutions ran in each wheel type (two-way ANOVA with repeated measures; wheel: $F = 0.161$, $P = 0.861$; gender: $F = 1.353$, $P = 0.26$; interaction: $F = 0.279$, $P = 0.758$). Similarly, no significant difference was detected between the mean preference ranks of the three wheel types (NM = 1.75, EM = 2.3, IM = 1.95; Friedman's $\chi^2 = 3.1$, $P = 0.212$, $n = 20$). Overall, eight hamsters ran most in the NM wheel, five in the EM wheel, and seven in the IM wheel. This distribution is not significantly different from random (Table 1). Those three groups of animals did not significantly differ from one another in either the number of revolutions ran in their favourite wheel, the total number of revolutions ran in all wheels, or their weight gain over the first 20 days (Table 1). However, the NM hamsters did not perform as great a proportion of their running in their

Table 1 Parameters of wheel preference and wheel use by 10 male and 10 female Syrian hamsters

	Favourite wheel			
	No mesh	External mesh	Internal mesh	Statistics
Number				
Males	4	3	3	χ^2=0.200, *P*=0.905
Females	4	2	4	χ^2=0.800, *P*=0.607
Total	8	5	7	χ^2=0.700, *P*=0.705
Revolutions/day in favourite wheel				
Males	4502±1060	6467±1423	5162±1360	Gender: *F*=17.81, *P*=0.001
Females	3035±682	3586±477	3688±622	Wheel: *F*=2.47, *P*=0.121
				Interaction: *F*=0.91, *P*=0.43
% revolutions/day in favourite wheel				
Males	47.3±8.8	70.3±9.9	64.0±4.6	Gender: *F*=39.95, *P*<0.001
Females	38.0±5.0	40.0±5.7	45.3±4.0	Wheel: *F*=7.98, *P*=0.005
				Interaction: *F*=3.78, *P*=0.05
Revolutions/day in all wheels				
Males	9525±1687	9154±799	8012±1684	Gender: *F*=0.67, *P*=0.425
Females	7880±983	8907±56	8250±1933	Wheel: *F*=0.59, *P*=0.569
				Interaction: *F*=0.84, *P*=0.46
Weight gain (g)				
Males	12.1±9.3	15.1±13.9	33.7±4.2	Gender: *F*=24.00, *P*<0.001
Females	34.8±8.4	48.8±0.07	35.7±6.9	Wheel: *F*=3.42, *P*=0.062
				Interaction: *F*=5.26, *P*=0.02

The statistics are from χ^2 tests and two-way ANOVAs

favourite wheel as the EM or IM hamsters did in theirs (Table 1). As compared with females, males performed a greater percentage of their running in their favourite wheel and gained less weight (Table 1).

The position of the nest was sufficiently consistent from day to day (consistent = more than 70% of all sightings) to establish which cage was the nest cage for each hamster. Thirteen of the 20 hamsters set up their nest in the end cage that had the water bottle, five in the other end cage, and two in the middle cage, a significant effect of cage position on nest position ($\chi^2 = 9.7$, $P < 0.01$). Eight hamsters had their nest where the preferred wheel was, seven where the least preferred wheel was, and five where the intermediate wheel was, a non-significant relationship between nest position and position of the preferred wheel ($\chi^2 = 0.951$, $P > 0.5$).

Nine hamsters (five males, four females) preferred the wheel that was in the end cage with the water bottle, nine (five males, four females) in the end cage without the water bottle, and two (both female) in the middle cage, a tendency towards a significant relationship between cage position and position of the preferred wheel ($\chi^2 = 4.9$, $P = 0.086$). This tendency is also hinted at by an ANOVA on the average number of wheel revolutions, mostly on the strength of the males' behaviour (end cage with water bottle: 3537±2451 for males and 2696±938 for females; middle cage: 1884±743 for males and 2516±832 for females; end cage without a water bottle: 3540±2007 for males and 3020±778 for females; cage type: $F = 2.357$, $P = 0.109$; gender: $F = 1.353$, $P = 0.260$; interaction: $F = 1.045$, $P = 0.362$). If the two end positions are combined, then there is a significant preference for wheels that were in end cages ($\chi^2 = 4.9$, $P = 0.025$). In pairwise comparisons between the wheel types that were in end cages, for the 18 hamsters that preferred a wheel in end cages, the ratios of preference were: 4 NM:1 IM, 6 IM:1 EM, and 3 EM:3 NM, a somewhat circular hierarchy of preferences that fails to show a clear overall favourite.

Of the seven hamsters that had preferred the NM wheel during the five days that just preceded the wheel block, four ran most in the IM wheel and three in the EM wheel during the block. Of the six that had preferred the EM wheel, three ran most in the NM and three in the IM wheel during the block. Of the seven that had preferred the IM wheel, five ran most in the NM and two in the EM wheel during the wheel block. None of these splits is significant on binomial tests ($P>0.2$, but note that the sample sizes are small). Males ran more overall during the period of wheel block than before (119% of pre-block levels on average), but females ran less (86% of pre-block levels).

Once their old favourite wheel was unlocked, males slightly reduced their overall running (to 110% of the pre-block levels), whereas females increased theirs to 103% of pre-block levels. Half (10/20) of the hamsters went back to their original wheel preference. Of the remaining 10 hamsters, five maintained the preference developed during the wheel block, and five now ran more in the wheel they had never preferred until then. The 10 hamsters that went back to their original choice had not initially expressed a stronger preference for their wheel, in terms of the percentage of total revolutions made in their favourite wheel during the first 20 days of the experiment, than the 10 hamsters that eventually developed a new preference ($47.4 \pm 7.1\%$ versus $53.2 \pm 17.1\%$, respectively; $F = 0.102$, $P = 0.754$).

Scabs were observed on the feet of almost all hamsters, but skin injuries on the legs were never seen. (Hamsters encounter wheels for the first time in their life when they arrive in our laboratory. They immediately start running a lot (Figure 1) and a scab invariably appears on the sole of one or two of their feet. These scabs generally disappear or turn into calluses within 40 days.)

Discussion

We found no evidence of a consistent preference for any given running surface. Although some individuals developed a strong preference for a particular wheel, all wheels were used to some degree by all animals, especially so in females. Moreover, at the group level there was no significant choice. No pattern emerged during the wheel block either. And following the wheel block, only half of the animals resumed their initial preference for a wheel.

We did find some evidence (a statistical tendency) of a preference for wheels in end cages (nine wheels preferred in each of the two end cages against only two in the middle cage). This mirrors a preference for building nests in end cages (Reebs & Maillet 2003; this study), though we found no significant association between nest position and preferred wheel position; hamsters with a nest in one end cage sometimes chose the wheel in that cage and sometimes chose the wheel in the other end cage. This tendency to prefer end cages is difficult to explain, but it is consistent with two conclusions relative to wheel-type preference: (1) there is simply no wheel-type preference; or (2) there is a wheel-type preference, but it was much weaker than the cage preference and was masked by it. We favour the first of these conclusions based on the lack of a clear hierarchy of wheel-type preferences in pairwise comparisons between end cages, on the fairly even use of all wheels by females, on the lack of any clear preference when the favourite wheel was locked and the number of wheels available was reduced to two, and on the fact that only half of the hamsters resumed their old preference when the favourite was made available again.

Males and females differed in a number of parameters. Individual females tended to use all three wheels more evenly than individual males. Females decreased overall running levels during the blocking of their favourite wheel, and increased them after the wheel was unblocked, whereas males showed the reverse pattern. However, even when each sex is taken separately, no significant preference for any given wheel surface emerges.

This lack of preference and the absence of skin injuries on the side of the legs of the animals lead us to conclude that wheels of the type we used here, with a larger diameter and a smaller between-rod interval than in Mrosovsky *et al*. (1998), would not benefit from the addition of plastic mesh. On the other hand, adding mesh would not necessarily be detrimental either, as the hamsters did not avoid such a running surface, and cautious researchers might want to use mesh anyway, especially for younger hamsters (smaller feet) than the ones we studied. In such a case, our results suggest that it would not matter whether the mesh is installed inside or outside the wheel. However, we should point out that some of our hamsters chewed on the plastic mesh, though never to a great extent. Concerns about the presence of bits of plastic inside the digestive tract must be taken into account when deciding whether to use plastic mesh or not. Replacing the mesh with a more solid and uniform sheet of plastic may not solve the problem, since previous work has shown that smooth running surfaces tend to be avoided, at least by laboratory mice (Kavanau & Brant 1965, Banjanin & Mrosovsky 2000).

Wheel diameter experiment

Material and methods

This experiment was similar to the previous one, except for the following. Ten new male hamsters (Charles River Canada) were placed individually in two-cage systems linked by a tunnel. One cage was of similar dimensions, with a similar wheel (35 cm diameter) as in the previous experiment. The second cage was smaller (Nalgene L-size for mice, $18 \times 34 \times 14$ cm) with a smaller wheel (L-size for mice, 23 cm diameter, 7.5 cm width, rods 2 mm thick separated by 5 mm of open space). Plastic mesh was placed on the inside of both wheels (whose rods were not similarly spaced) to limit the difference between them to diameter and width. The water bottle was attached to the large cage only.

Five of these 10 hamsters were 60 days old and had just arrived in our laboratory. The other five were 105 days old and had been used in another experiment (the one with platforms, presented below). The experiment was repeated with 10 females (also 60 and 105 days old, Charles River Canada) after the equipment was thoroughly washed.

Because the wheels were of different diameters, all calculations were made on meters ran per day rather than on wheel revolutions per day.

Results

All 10 males ($P = 0.001$ on a binomial test) and eight of 10 females ($P = 0.0547$) ran more in the large wheel than in the small one during the first 20 days. The preference was very clear for males: on average they ran $86 \pm 17.8\%$ of their total daily mileage in the large wheel. Female preference was less marked: the eight females that preferred the large wheel ran $72 \pm 10.7\%$ of their daily mileage on average in this wheel (the other two females ran 66% and 67% of their daily mileage in the small wheel). The percentage of distance ran in the preferred wheel was significantly higher for males than for females ($t = 2.321$, $P = 0.032$).

When the preferred wheel was blocked for 10 days, the hamsters made some use of the non-preferred wheel (on average, the total distance ran per day dropped to 59% and 52% of its original level for males and females, respectively, and these values are also representative of the two females that had preferred the small wheel). When the preferred wheel was made available again, the daily mileage ran bounced back to 124% and 73% of the pre-block level for males and females, respectively. All hamsters returned to their old, strong wheel preference, except for one of the two females that had preferred the small wheel originally; that female now ran more in the large wheel.

Eleven hamsters nested in both the larger and smaller cages, almost equally often (no more than 70% of all sightings). In eight out of the nine other hamsters where a consistent intra-individual preference was shown (more than 75% of sightings in the same cage), the nest was in the smaller cage. Faeces were always observed in both cages.

Discussion

The apparatus used in this experiment was not ideal because the two cages did not differ only in their wheel size; the cages themselves were of different dimensions (Nalgene's L-size wheels are built to fit only on L-size cages, and F-size wheels on F-size cages), and only the larger cage had a water bottle. Therefore, it could be argued that the strong wheel preference we observed is only the consequence of a preference for larger cages or for proximity to a water bottle. While we cannot completely discount this possibility, we consider it unlikely for the following reasons: (1) for slightly more than half of the hamsters, nest position indicated no cage preference (there were nests in both cages simultaneously), and for the remainder the preference was for the small cage, not the large cage – even though the latter is where their preferred wheel was; (2) results from the plastic mesh experiment revealed no wheel preference between an end cage with a water bottle and an end cage without a water bottle; and (3) one would expect wheel preference, if it exists, to be based more on wheel characteristics than on cage size.

The hamsters used in the experiment were of two different ages and levels of experience. This did not seem to be a factor in the results, as all males and almost all females (four of one age/experience and four of the other) expressed the same preference.

As in the previous experiment, females ran more evenly in the wheels, but preference for the wheel with the largest diameter was still clear for both sexes. Moreover, getting used to the smaller wheel (during the block period) was not enough to reverse this preference. The conclusion of Mrosovsky *et al*. (1998) about larger wheels being preferred can therefore be extended to wheels twice as large as the largest wheel (17.5 cm diameter) they tested, and to both sexes. Preferences for larger wheels have also been noted in mice, though only males were tested (Banjanin & Mrosovsky 2000, Deboer & Tobler 2000).

The main disadvantage of smaller wheels is probably that the hamsters must run with their back arched in an unnatural and possibly uncomfortable way. Of course, large wheels have a drawback too: they take up more space and may not entirely fit inside a cage (and if they protrude, they must be made escape-proof, a necessity with hamsters). It is noteworthy that the equipment we use in our laboratory is manufactured to house rats, and so one rule of thumb may be to use rat wheels for hamsters. The Canadian Council on Animal Care (1984) recommends the use of standard rat cages for Syrian hamsters.

Platform-in-wheel experiment

Material and methods

This experiment was similar to the previous one, except for the following. Ten new male hamsters (Charles River Canada) were again placed individually in two-cage systems linked by a tunnel. Both cages and attendant wheels were Nalgene F-size for rats. One of these wheels (hereafter called 'truncated') had a 26 cm long plastic platform wedged inside. Therefore, one part of the wheel was circular and the other part was flat. The platform divided the 17.5 cm radius of the wheel into a 11.25 cm open space between it and the hub of the wheel, and a 6.25 cm space underneath it; this smaller space was blocked with an additional piece of plastic so that the hamster could not access it. The platform and plastic block unbalanced the wheel, making it harder to run while the platform was being swung up, and easier when the platform was being swung down. Plastic mesh was placed on the inside of both wheels; thus, in the platform wheel, plastic mesh covered both the platform and the rods, providing a relatively constant running surface similar to that of the regular wheel. The water bottle was attached to one of the two cages, determined at random.

Five of these 10 hamsters were 60 days old and had just arrived in our laboratory. The other five were 105 days old and had been used in another experiment (the one on wheel diameter presented above). The experiment was repeated with 10 females (60 and 105 days old, Charles River Canada) after the equipment was thoroughly washed.

Because the wheels were of different shapes, calculations were made on metres ran per day rather than on wheel revolutions per day.

Results

All 10 males ($P = 0.001$ on a binomial test) and all 10 females ran more in the normal wheel than in the truncated one during the first 20 days. On average, males and females, respectively, ran $99 \pm 1.0\%$ and $88 \pm 8.8\%$ of their total daily mileage in the normal wheel. This difference between males and females is significant ($t = 3.892$, $P = 0.001$).

When the preferred wheel was blocked for 10 days, the hamsters made some use of the non-preferred, truncated wheel (on average, the total distance ran per day dropped to 53% and 49% of its original level for males and females, respectively). When the preferred wheel was made available again, the daily mileage ran bounced back to 114% and 106% of the pre-block level for males and females, respectively. Moreover, all hamsters returned to their old, strong wheel preference.

All 10 males and eight out of 10 females were seen more often nesting in the cage with the truncated wheel.

Discussion

Canyon mice (*Peromyscus crinitus*; Kavanau & Brant 1965) and deer mice (*P. maniculatus*; Kavanau 1966, 1967) can develop preferences for square wheels, but only if they are first forced to use them. In our laboratory we could not make a square wheel big enough to accommodate a hamster; so instead we made a truncated wheel by simply adding a platform. The hamsters clearly avoided that design if they had a choice. (The fact that the hamsters were of two different age groups did not affect the results, as all animals showed the same strong preference for the normal wheel.) Even after being forced to use the modified wheel for 10 days (and doing so to a fair extent), the hamsters returned to a normal wheel when given a choice. The difference between our results and those from the *Peromyscus* studies could reflect different jumping abilities. Square wheels, and to a certain extent the platform wheel we used, require the running animal to jump at the corners, and hamsters are not known as nimble jumpers, whereas *Peromyscus* mice are.

On the other hand, maybe hamsters simply did not like the fact that the truncated wheel was unbalanced (the square wheels in Kavanau & Brant 1965 and Kavanau 1966, 1967 were well balanced). In the next experiment, we better imitated another one of Kavanau's (1966, 1967) unusual wheels. Deer mice were shown to develop a preference for wheels 25 cm in diameter, with four 'hurdles' 1.9 cm high (Kavanau 1966, 1967). We offered our hamsters 35 cm wheels with two 'speed bumps' 1.5 cm high.

Speed bumps experiment

Material and methods

At the end of each of the two preceding experiments, the 10 males and 10 females (all of them 150 days old by then) were placed in sets of two F-size cages linked by a tunnel, and offered a choice between two F-size wheels, one of which had two 'speed bumps' installed at diametrically opposed points along the running surface. Each speed bump consisted of a wood dowel split in half, creating a hemisphere 3 cm in diameter (width of the speed bump) and 1.5 cm in radius (height). The length of the speed bump covered the full width of the running surface. A plastic mesh covered the inside of both wheels, hugging the speed bumps fairly closely in the modified wheel. The number of wheel revolutions was noted every day for 10 days.

Results

Some hamsters expressed a strong preference, though this preference could be for the normal or the modified wheel (e.g. males Nos 3, 4, 6 and females Nos 2, 3, 6 in Figure 2). Other hamsters used both wheels more or less equally (Figure 2). Overall, five out of 10 males and six out of 10 females ran more in the modified wheel ($P > 0.35$ on binomial tests). No relationship was detected between wheel preference and which experiment (diameter or platform) the hamster had just come from before starting

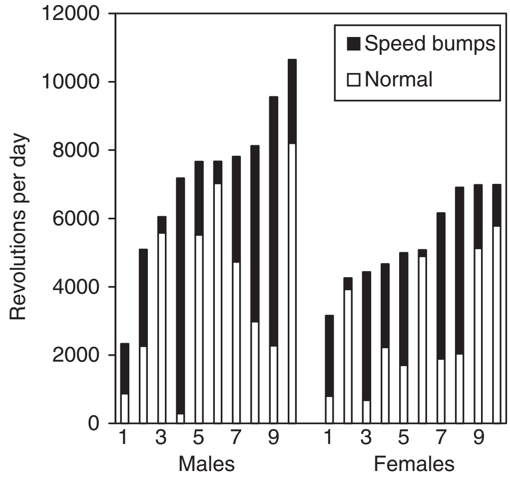

Figure 2 Number of daily wheel revolutions, averaged over 10 days, by individual male and female Syrian hamsters that had simultaneous access to two running wheels: one with a running surface made of plastic mesh over evenly spaced rods 9 mm apart (normal), and one with two 'speed bumps' installed underneath the mesh at diametrically opposed points

this experiment ($\chi^2 = 0.202$, $P > 0.5$). No significant difference was detected between the two wheel types in the number of revolutions ran in them (two-way ANOVA on repeated measures, $F = 0.460$, $P = 0.5$). On average, males and females, respectively, ran $75 \pm 13\%$ and $76 \pm 15\%$ of their total daily mileage in their favourite wheel, a non-significant difference between the sexes ($t = 0.238$, $P = 0.814$). Males, however, ran more than females ($F = 4.781$, $P = 0.042$).

Discussion

This experiment and the previous one with truncated wheels essentially represent failures to enrich the running wheel environment for hamsters. Hamsters avoided the truncated wheel, and at the group level neither favoured nor avoided the speed bump design. Kavanau (1967) explained the success of his modified wheels by suggesting a propensity in deer mice for acrobatics that involved jumping. Hamsters in contrast, though excellent climbers and escape artists, are not good jumpers. Interestingly, Kavanau (1966) reported that house mice, *Mus musculus*, are less prone to vigorous exercise than deer mice, and like hamsters they do not tend to prefer wheels with hurdles.

General discussion

In terms of overall preference, males and females yielded the same conclusions, but in three of the four experiments males ran a greater proportion of total mileage in their favourite wheel. Females appeared to be less specialized (see Guerra & Ades 2002 for another example of male–female difference in task performance by hamsters). We have no explanation for this difference. Nevertheless, the existence of such a difference shows that testing both sexes is advisable in animal welfare studies.

There was no relationship between nest position and preferred wheel in our experiment with three-cage systems, probably a consequence of hamsters preferring to nest at the end of a linear array of cages and the fact that we systematically varied wheel position along the array. In the two-cage systems, there seemed to be a tendency for hamsters to nest next to the less preferred wheel, though this may have had nothing to do with the wheel *per se*. Nesting next to the small wheel also meant nesting in the smaller cage, and hamsters seem to prefer constrained areas for nesting. Nesting next to the truncated wheel meant nesting in a darker cage, as the platform added shade to the cage, and hamsters prefer dark areas for sleeping.

In our experiments with plastic mesh and speed bumps, many subjects used all wheels more or less evenly. One might ask whether hamsters value such diversity in running wheel access. One study with operant costs of access to resources (Sherwin 1998) showed that mice with simultaneous access to tunnels and wheels as opportunities for locomotion end up disregarding the tunnels with time and increased costs of access. It might be interesting in future studies to see whether hamsters would similarly end up disregarding some of the wheels they had originally used, as long as at least one good type of wheel remains available.

Similarly, a study with operant costs of access to resources could give us information on how much the hamsters value larger wheels. Our result that hamsters reduced their running by half when the 35 cm wheel was blocked and only the 23 cm wheel was available suggests that hamsters value larger wheels fairly highly. A study with operant costs could provide valuable confirmation.

Finally, we point out that, as in all studies based only on choice tests, our results give insight on how to improve the psychological welfare of hamsters, but remain silent on any possible long-term health benefits. There is no reason to believe that hamsters know what is best for them in terms of long-term health benefits in a laboratory setting. Admittedly, running in a wheel that is too small could cause back problems. On the other hand, too much running because a comfortably large wheel is the only 'toy' in the cage could lead to excessive weight loss and foot injuries. Perhaps the best solution would be a comfortable (i.e. preferred) wheel whose access is limited, or whose attraction is diverted by other cage improvements, if and when the hamsters show signs of debilitatingly high running levels. Only long-term monitoring of health conditions in a large sample size of hamsters having access to various single wheel types could address this question.

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