

REPETITIVE BACKFLIPPING BEHAVIOUR IN CAPTIVE ROOF RATS (*RATTUS RATTUS*) AND THE EFFECTS OF CAGE ENRICHMENT

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Abstract

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Repetitive 'stereotyped' behaviours are often performed by both wild and domestic rodents in small laboratory cages. In this study, a behaviour resembling a backwards somersault or backflip is described and quantified in captive roof rats (ship or black rats, Rattus rattus). Videotapes of captive-bred rat pups showed that repetitive backflipping developed rapidly after weaning. In all subjects, the behaviour was highly cyclical, with more than 90 per cent occurring during the dark phase of the light:dark cycle. Individual variability in the performance of backflipping was considerable but performance levels for each individual were consistent from day to day and at 30 and 60 days of age. Highly significant differences were found between litters (families), indicating important maternal and/or genetic effects on performance levels. Cage enrichment in the form of a wooden nest box resulted in dramatically lower rates of performance. Increased cage height resulted in delayed development of backflipping, as well as changes in the form of the behaviour. Results are consistent with the hypothesis that the development and expression of backflipping in young roof rats may be triggered by weaning and maintained by a heightened state of arousal in a relatively impoverished environment with limited opportunities for perceptual and locomotor stimulation.

Keywords: *animal welfare, development, environmental enrichment, roof rat, stereotyped behaviour*

Introduction

A number of rodent species are known to display repetitive stereotyped behaviours when housed in small laboratory cages. Odberg (1986) and Wurbel *et al* (1996) have described a repetitive jumping behaviour in bank voles (*Clethrionomys glareolus*) and laboratory mice (*Mus domesticus*) which is characterized by jumping straight up and down, usually in a corner of their cage. Cooper and Nicol (1991) observed repetitive rearing by voles in which the animals stood on their hind legs at a preferred location in the cage with forepaws resting on the cage wall; repetitive 'looping' which involved somersaulting from the wire cage-top; and repetitive 'weaving' which involved pacing to and fro over the same point, with frequent rearing during

turning. Repetitive bar gnawing has been reported in captive gerbils (*Meriones unguiculatus*; Elwood & Broom 1978; Wiedenmayer 1997a), golden hamsters (*Mesocricetus auratus*; Arnold & Estep 1993) and laboratory mice (Wurbel *et al* 1996). Wiedenmayer (1997b) has also reported repetitive digging in laboratory-housed gerbils.

Many repetitive behaviours in caged rodents develop at the time of weaning (Wurbel *et al* 1996; Wiedenmayer 1997a, b). Wurbel and Stauffacher (1997) proposed that thwarted suckling associated with artificial weaning in laboratory mice triggers increased levels of exploratory and escape behaviours. They hypothesized that increased exploratory and escape behaviours occurring at the time of artificial weaning are the source behaviours from which repetitive behaviours such as bar gnawing develop in caged mice. Stereotypic wire-gnawing was negatively correlated with weaning weight; mice with low weaning weight showed more escape behaviour and developed a higher degree of stereotypic performance than mice of relatively high weaning weight.

Changes in cage size and the addition of environmental enrichment devices have been used with mixed success to reduce repetitive behaviours in caged rodents. Odberg (1987) reduced the incidence of repetitive jumping behaviour in captive bank voles by adding clumps of intertwined twigs to their cages. However, repetitive locomotor behaviours were more difficult to disrupt through environmental enrichment in older voles (Cooper *et al* 1996). Wiedenmayer (1996), working with gerbils, found that increasing cage size four-fold had no effect on the ontogeny of stereotyped digging.

Providing some form of shelter is a common method of enriching the cages of captive rodents (Van de Weerd & Baumans 1995). Both rats and mice were found to prefer cages with shelters to cages without shelters (Townsend 1997; Manser *et al* 1998; Van de Weerd *et al* 1998). Arousal or fear evoked by extraneous stimulation in the laboratory environment, such as interactions with human caretakers, sudden loud noises, being placed in a new cage and stimuli from neighbouring animals, may evoke escape responses in young rodents. A shelter or nest box can insulate animals from such extraneous stimulation and provides a means of escape, thereby offering the animal a degree of control over its environment. To the extent that arousal or fear (ie motivation to escape) can contribute to the development and expression of repetitive motor behaviours in captive rodents and the use of shelters can attenuate arousal or fear, provision of such structures in laboratory cages may be a means of reducing the incidence of such behaviours. Chamove (1989) and Townsend (1997) reported that mice and rats, respectively, were less fearful if reared in cages with shelters. Hansen and Damgaard (1991) found that the physiological stress levels of farmed mink (*Mustela vison*) increased when deprived of nest boxes in their cages. Wiedenmayer (1997c) demonstrated that young gerbils given access to an artificial burrow did not develop repetitive digging behaviour in contrast to those reared on sand without burrows.

Species that spend a relatively large amount of time foraging over a large area might be most sensitive to spatial restriction. Draper and Bernstein (1963) found that increasing available vertical space was effective at reducing a stereotyped locomotor behaviour in a feral, arboreal species of monkey (rhesus macaque, *Macaca mulatta*).

The purpose of this investigation was to describe the performance of a repetitive locomotor pattern which resembles a backwards somersault or backflip in first generation captive-born roof rats (ship or black rats, *Rattus rattus*) and then to determine the effects of two forms of cage enrichment – provision of shelter and cage enlargement – on the development and expression of this behaviour. Diurnal cyclicality, sex differences, inter- and intra-individual variability in performance rates and litter (family) differences were quantified.

Subjects and methods

Animals

On three occasions, adult roof rats were captured from field pens maintained by the Department of Wildlife, Fish and Conservation Biology at the University of California, Davis, USA. Approximately 50 per cent of the wild-caught rats bred successfully in captivity. They will be referred to henceforth as 'breeders' or 'parents' of the subjects of this study. Breeders were housed in opposite-sex pairs in 25x76x20 cm *lxwxh* wire mesh cages in a 6.1x4.3x2.5 m *lxwxh*, air-conditioned room. Shavings and paper towels were provided as bedding. The rats were fed standard Rat Chow (Purina, Richmond, USA) and provided with water *ad libitum*. All cages received food supplementation twice a week in the form of fresh produce and occasionally peanut butter, crackers, dog food, Monkey Chow (Purina, Richmond, USA) and marshmallows. Room temperature was maintained at 23.3°C and the light:dark cycle was 18:6, with lights on at 0215h. A relatively long light period was maintained in order to stimulate breeding. Two 25 watt red light bulbs remained lit continuously throughout the study to permit videotaping during the dark period (2015–0215h).

Subjects (F1 generation) were obtained from litters containing at least two pups of the same sex so that each subject could be housed with a same-sex littermate. Pups were weighed starting on day 21 and weaned when they weighed approximately 56g. Age at weaning ranged from 21 to 27 days (mean of 24 days).

A maximum of two males and two females were retained from each litter; surplus young were humanely euthanased. Subjects were weaned in same-sex sibling pairs into wire mesh cages identical to those described above for breeders unless the experiment had different housing requirements. At the time of weaning, all subjects were anaesthetized briefly by inhaling vapours of Metafane® (methoxyflurane; Schering-Plough, Omaha, USA) and each received a distinguishing ear mark. While anaesthetized, one member of each pair was dyed black with Nyanzol dye (Nyanza Inc, Lawrence, USA) for ease of identification during videotaping.

Recording

Subjects were videotaped in their home cages using a Panasonic 6010 time-lapse video recorder (California Video Sales Inc, Sacramento, USA) and an RCA (Model #TC1005) low-light silicon diode camera (RCA Closed Circuit Video Equipment, Lancaster, USA). Unless otherwise stated, backflips viewed on videotapes were transcribed with a Macintosh Powerbook 180c, using two programs specifically written for this purpose. Both programs provided a running tally of the number of backflips the subject performed in each interval that was viewed. Subjects were classified as backflippers whenever they repeated the same series of locomotor movements, contacting three or more cage surfaces three or more times within 1min on two or more occasions within a videotaping session.

Each tape was viewed three times. The first viewing determined those minute intervals in which the subjects were active ('active minutes') and the motor patterns associated with the repetitive behaviour were described. All instances of backflipping were counted during the second and third viewings. Only one sibling of each pair was observed and scored during each viewing. Inter- and intra-observer reliability estimates were > 95 per cent.

Experiment 1a: incidence of backflipping at the time of weaning

The goal of this experiment was to determine when, after weaning, young rats begin to exhibit backflips. This required the development of an ethogram which included all components of the stereotyped backflipping behaviour. Identifying components of backflipping behaviour allowed for the possibility that each subject might perform slightly different locomotor patterns.

Thirteen male sibling pairs (26 subjects) were obtained from 10 different breeding pairs. They were weaned at 22–25 days and placed in standard wire mesh cages, as previously described. Since backflips were first observed in the days following weaning and not before, it seemed likely that the behaviour developed at that time. Videotapes of four litters prior to weaning revealed no instances of backflipping by the young or their parents. However, some pups not used in this research and weaned late developed repetitive backflipping while still housed with their parents. Each pair in this experiment was videotaped for 12h, starting at 1800h and ending at 0600h on the first night after weaning. During tape transcription, all locomotor patterns that involved contacting more than one cage surface were recorded. Listed below is a description of the four major physical movements involved in backflipping:

jump – subject actively leaps (propelling itself with its hind legs) from the floor to either the wall or ceiling, or from the wall or ceiling to the floor, always leading with the front feet (ie if the subject jumps to the ceiling or floor, its head and front feet contact the ceiling, or floor, first).

wall contact ('wall') – subject clings to a wall with all four feet.

ceiling contact ('ceiling') – subject clings to the ceiling with all four feet.

drop – subject passively drops head first from either wall or ceiling, front feet contacting the floor first.

In most cases, these four components were performed in the order listed above to meet the criteria for backflipping (jump-wall-ceiling-drop), although the behaviour often did not commence with a jump but rather the subject simply climbed onto the wall (wall-ceiling-drop). Also, some subjects would climb down from the ceiling to an adjoining wall before dropping to the floor (wall-ceiling-wall-drop).

All instances of these four behaviours were tallied using an NEC Multispeed™ laptop computer (NEC, Wood Dale, USA) and the Observer behavioural data collection program (Noldus Information Technology BV, Wageningen, The Netherlands). Each subject was recorded as having performed a repetitive backflipping sequence when it engaged in the same sequence of locomotor events (eg wall-ceiling-drop) at least three times in 1min on two or more instances within a videotaping session. Data recording was terminated once the subject had performed the behaviour to criterion.

Experiment 1b: inter-individual variation and cyclicity of repetitive backflipping

Two male and two female pups were obtained from each of eight pairs of breeders and housed in standard wire-mesh cages. Subjects were videotaped for a 24h period at approximately 30 days of age, starting at least 72h after weaning. Backflipping was recorded in bouts. A bout was defined as a series of flips where the inter-flip interval was 3s or less. Preliminary observations had shown that when the inter-flip interval was greater than 3s the animal often rested or engaged in other activities. Some bouts consisted of only one flip. The mean and range of flips per bout were obtained, as well as the total number of bouts and total number of flips exhibited in a 24h period. From these data, it was possible to determine if there was a diurnal cycle to the activity. In addition, comparisons were made between sexes and between cagemates (sibs).

Time interval sampling was used in which the videotape was divided into 20s segments and all instances of the behaviour were counted. Twenty second intervals were used because that interval length was associated with the highest intra-observer reliability scores during preliminary studies. Taping commenced at 1830h every other day.

Sex differences in total number of backflips were analysed with the students *t*-test. Pearson's product moment correlation coefficients were calculated to determine if cagemates performed similarly.

Experiment 1c: intra-individual variability over two successive days

Four male sibling pairs (eight subjects) were obtained from four different breeding pairs and subjected to the same post-weaning housing conditions described previously.

Since most backflipping occurred during the hours of darkness, subjects were videotaped from 1800–0600h on two consecutive nights and data were compiled for 1900–0600h. Video records from 1800–1900h were omitted to minimize any effects of disturbing the animals by setting up the camera equipment.

As previously described, each tape was viewed three times. However, instead of counting all backflips, five randomly selected 1min samples were counted for each hour and averaged to obtain a rate per minute for each hour. These are referred to as '5min means'. Each hour's 5min mean was multiplied by the number of active minutes in that hour to obtain a rough estimate of the number of backflips the subject performed during that hour. Hourly estimates were added together to obtain an estimated nightly total. Hourly estimates were compared with actual counts for 12 randomly selected subjects in the baseline condition (experiment 1b). Estimates were highly correlated with actual totals ($r = 0.99$, $P < 0.001$). Because of the high degree of correlation, this method was used to estimate performance totals in this and subsequent experiments.

The two nightly totals for the subjects in this experiment were compared statistically using a *t*-test for related samples (matched pairs). Pearson's product moment correlation coefficients were computed for the two nightly totals for the eight subjects.

Experiment 1d: performance at 30 and 60 days of age

Eight male sibling pairs (16 subjects) were obtained from eight breeder pairs and housed as previously described. Subjects were videotaped from 1800–0600h at 30 and 60 days of age and data were recorded as described for experiment 1c. Data obtained at 30 and 60 days of age were compared using a *t*-test for related samples (matched pairs). In addition, Pearson's product moment correlation coefficients were obtained for individual performance at 30 and 60 days of age.

Experiment 1e: within- and between-litter (family) differences

A total of 36 male subjects were used; 4 subjects were obtained from each of 9 litters from 9 different breeding pairs. Subjects were housed in pairs in standard wire-mesh cages as previously described.

At approximately 30 days of age, both pairs of littermates were videotaped within 72h. Nightly performance rates were estimated from 5min means as described previously. Subjects' nightly totals were log transformed due to skewness. These transformed totals were compared within and between litters (ie families) with maximum likelihood estimates using a nested, mixed model ANOVA. A variance components' analysis was also performed to compare the relative magnitude of the variance attributed to family versus animal-to-animal differences. A Pearson's product moment correlation was obtained to determine whether the averaged performance estimates of sibs housed in separate cages were correlated, providing another measure of family resemblance.

Experiment 2: effects of providing a shelter on the expression of backflipping behaviour

Twenty-eight male subjects were acquired from 10 breeding pairs for this experiment. Eleven female sibling pairs (22 subjects) were used as controls (no shelters).

Wooden nest boxes (13x25x20 cm *lxwxh*) were placed inside standard wire-mesh cages and two male littermate subjects were weaned into each cage. When available, two female littermates were weaned into standard cages without nest boxes as controls. At approximately 30 days of age, the subjects were videotaped for a 12h period, from 1800–0600h, as previously described for experiment 1c. Nightly performance rates were estimated as described in experiment 1c. Shelter-housed subjects were compared with controls using a *t*-test for independent means.

Experiment 3: effects of increased cage height on expression of backflipping behaviour

Eight male sibling pairs (16 subjects) were obtained from seven breeding pairs. The rats were housed in conditions identical to experiment 1, except that the cage height was increased from 20 to 91 cm.

All 16 subjects were placed in the enlarged cages at the time of weaning. The first six subjects (three pairs) were videotaped at 30 days of age only. The remaining 10 subjects (5 pairs) were taped at 30 days and again at approximately 60 days of age after a caretaker witnessed them performing a circling behaviour which conformed to our previously-stated definition of a repetitive behaviour. Data collection proceeded as described in experiment 1c. After the second taping at 60 days, these five pairs were placed in standard 25x76x20 cm cages to determine whether a reduction in cage size would affect the performance of backflipping behaviour.

Results

Experiment 1a

All of the subjects met the criterion for repetitive backflipping within the first 5h of videotaping on the first night after weaning. During the first hour of taping (1800–1900h), only 8 per cent of subjects met the criterion. This was in keeping with the prediction that activity levels would be low before the hours of darkness. Only 20 per cent had met the criterion by the end of the second hour (2000h), which ended the light period. During the next 2h (2000–2200h), the cumulative total reached 54 per cent, and by the end of the fifth hour (2300h, the third hour of darkness), 100 per cent of subjects had met the performance criterion.

At the start of taping, subjects moved around the cage contacting wall and ceiling and performing jumps and drops in a non-stereotyped manner. As time passed, subjects developed more consistent patterns of locomotion. Often the pattern started with climbing up one wall, followed by a ceiling contact which, in turn, was followed by a drop. By the end of 5h, this wall-ceiling-drop pattern had been performed to criterion by 24 of the 26 subjects; the other two subjects exhibited the jump-ceiling-drop locomotor pattern.

Patterns of locomotion were highly variable during the early stages of performance, with individuals occasionally contacting a second wall (wall-ceiling-wall-drop) or adding a jump (jump-wall-ceiling-drop). In this study, individuals often performed more than one version of the repetitive behaviour to criterion: 2 subjects (7%) performed four versions and 13 (50%) performed at least two versions during the first 5h.

Experiment 1b

The subjects in this experiment exhibited a number of different variations of repetitive backflipping. Some individuals performed a 'figure-of-eight' version in which the flip was performed at both ends of the cage, one being a mirror image of the other. Others performed variations of the simple 'wall-ceiling-drop' by adding a jump (jump-wall-ceiling-drop) or a wall contact (wall-ceiling-wall-drop).

Mean number and range of backflips, backflip bouts and backflips bout⁻¹ performed by male and female rats in a 24h period are summarized in Table 1. Total number of backflips and

backflip bouts varied greatly. Performance rates also varied greatly, with active subjects performing 3–64 backflips min^{-1} and 3–2256 flips h^{-1} . It is important to note that the maximum rate, about 1 backflip s^{-1} , was only maintained for about 1 min at a time. The range in number of backflips bout^{-1} was relatively low with an overall mean of 7.0.

Table 1 Number of backflips, backflip bouts and backflips bout^{-1} performed by male ($n = 20$) and female ($n = 20$) rats in a 24h period at approximately 30 days of age.

	Males	Females
Total backflips		
mean \pm SEM	4015 \pm 1109	5018 \pm 1218
range	214–11237	168–16421
Total backflip bouts		
mean \pm SEM	523 \pm 73	553 \pm 87
range	65–1029	68–1444
Backflips bout^{-1}		
mean \pm SEM	5.9 \pm 0.7	8.1 \pm 1.3
range	1–88	1–65

Males and females did not differ in total number of backflips ($P = 0.5$), total number of bouts ($P = 0.79$), or average number of flips bout^{-1} ($P = 0.15$). The total number of backflips performed by cagemates was highly correlated ($r = 0.76$, $P < 0.001$).

Figure 1 illustrates the number of backflips performed each hour by three selected subjects. Ninety-five per cent of all backflips occurred between 2000h and 0200h, during the dark period of the light:dark cycle. Almost without exception, subjects who performed the behaviour during the light hours (0200–2000h) were among the subjects with the highest total number of backflips. For example, the subject represented by the open (white) bars in Figure 1 performed the highest recorded number of flips (16 421). Thirty-eight per cent of these (6280) were performed during the light hours. The other two subjects presented in Figure 1 represent more typical performance rates. The subject represented by solid black bars performed its highest hourly total (740 flips) between 2200h and 2300h. In the following hour, this subject was inactive. The subject represented by the striped bars performed its highest rate (1650 flips) between 2100h and 2200h followed by a gradual decline in performance over the next 4h.

Experiment 1c

Estimated total number of backflips (mean \pm SEM) were similar for individuals over consecutive nights (day 1, 4590 \pm 1043; day 2, 4990 \pm 831; $P = 0.5$). Performance rates on nights 1 and 2 were correlated ($r = 0.83$, $P < 0.05$).

Experiment 1d

Estimated total number of backflips (mean \pm SEM) exhibited at 30 and 60 days (3620 \pm 741 and 4296 \pm 1052, respectively) were similar ($P = 0.33$). In addition, performance rates at the two ages were correlated ($r = 0.76$, $P < 0.001$).

Experiment 1e

Table 2 presents the mean total number of backflips night^{-1} for pairs of rats in each cage, as well as litter means. Cage means ranged from 1504 to 10 165 backflips night^{-1} . Standard errors

calculated for each litter using performance data for the four sibs were unexpectedly low (range of 15.4–24.7). The performance of rats from different litters differed significantly ($P < 0.01$). The variance components' analysis comparing the relative variances of litters and individuals showed that 21 per cent of the variance was attributable to family differences. Performance means for pairs of related siblings housed in separate cages were also correlated ($r = 0.78$, $P < 0.001$), lending support to the litter effect found with the ANOVA.

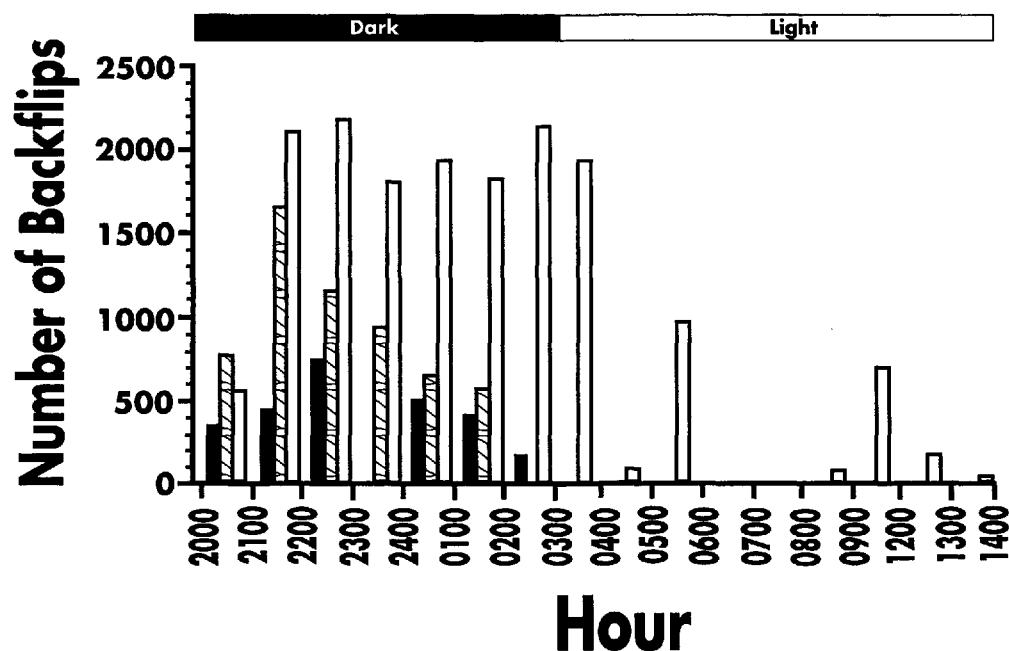


Figure 1 Number of backflips exhibited by three selected individuals during a 24h period at 30 days of age. Hours not shown indicate inactivity.

Table 2 Estimated cage and litter means \pm SEM for number of backflips exhibited by captive roof rats during an 11h period at 30 days of age.

Litter	Cage A	Cage B	Litter mean
1	1863	2244	2054 \pm 17.6*
2	1513	1504	1508 \pm 16.4
3	1305	2860	2082 \pm 24.0
4	2688	2786	2736 \pm 15.4
5	4391	5820	5106 \pm 15.4
6	10165	8180	9172 \pm 16.2
7	2848	6516	4682 \pm 24.7
8	3714	2812	3263 \pm 17.0
9	4636	3599	4118 \pm 19.6

*SEM calculated from individual totals.

Experiment 2

Figure 2 shows the frequency distribution of performance estimates for subjects in the experimental and control conditions. Shelter-housed subjects performed significantly fewer

(mean \pm SEM) flips than controls (1511 ± 366 vs 3477 ± 553 ; $P < 0.01$). As Figure 2 shows, 14 of 28 shelter-housed subjects (50%) performed 1000 or fewer backflips while only 4 of 22 control subjects (18%) performed 1000 flips or fewer. Nine of 22 control subjects (36%) performed more than 4000 flips, while none of 28 shelter-housed subjects exhibited this level of performance. Also, one pair of shelter-housed subjects did not meet the backflipping criterion. Interestingly, it was found that the siblings of this pair, who served as controls, also did not exhibit repetitive backflipping behaviour. These subjects were included in the analysis.

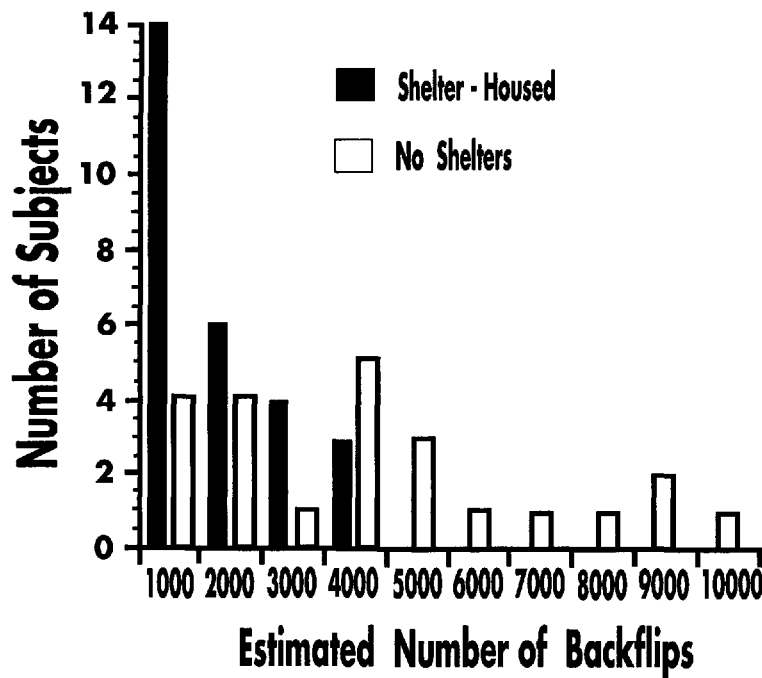


Figure 2 Number of subjects in shelter-housed ($n = 28$) and non-shelter-housed ($n = 22$) treatment groups performing various estimated numbers of backflips in a 12h period at 30 days of age.

Experiment 3

None of the 16 subjects performed repetitive backflipping at 30 days of age while in the enlarged cages. During the first taping, all subjects were observed to run up and down the walls of the cage, occasionally contacting ceiling and floor. Although some movement patterns were repeated more than once, none were ever repeated three or more times within 1min on two or more instances within a videotaping session.

All five pairs videotaped at 60 days of age performed a circling repetitive behaviour near the top of their cage. The animals jumped from wall-to-wall in a rhythmic, circular pattern at rates comparable to those seen for the backflip behaviour, but it was rare for them to contact the ceiling or floor. When performed at relatively high speeds, subjects only contacted the two opposing walls. When placed in standard 25x76x20 cm cages after 60 days of age, all 10 subjects displayed vertically-oriented backflips within 2 days.

Discussion

The results of experiment 1a indicate that repetitive backflipping developed at or around the time of artificial weaning. All subjects met the criterion for repetitive backflipping on the first night after weaning. While it is possible that subjects performed backflips prior to weaning, backflips were not seen in the four litters videotaped prior to weaning. It is important to note that individuals not removed from their parents at the normal time for weaning eventually performed repetitive backflipping behaviour while still housed with their parents. These observations suggested that artificial weaning may have triggered the development and/or expression of the behaviour at an earlier age than it would have otherwise occurred. Wurbel and Stauffacher (1997) proposed that the artificial separation of young mice from their parents at an early stage of development, when suckling motivation is high, may trigger increased levels of exploratory and possibly escape behaviours. Similarly, being placed in an unfamiliar 'novel' cage environment may trigger an increase in exploration and/or escape responses. Locomotor activities associated with exploration and escape may then become the source behaviours for the development of repetitive stereotyped behaviours. In addition, handling by humans at the time of weaning may contribute to a heightened state of arousal.

Another observation also supports the hypothesis that weaning represents an important benchmark in the development of repetitive stereotyped behaviours in captive rodents. Although backflips were not observed prior to weaning in the present study, rat pups were very active, often jumping and crawling on the walls and ceiling of their cage. They were also observed to exhibit play behaviours, and on three separate instances pups were observed to jump onto a parent's back and 'ride' for a few seconds. This is in marked contrast to the pups' post-weaning behaviour in which play behaviours were never seen and social interactions with their cagemates were infrequent.

Considerable individual variation has been noted in the performance of repetitive stereotyped behaviours in voles (Odberg 1986), pigs (Rushen 1984) and mink (Mason 1993). In the present study, the highly variable levels of backflipping behaviour in different roof rats, coupled with the consistency of individual performance over time, indicates that each animal establishes its own level of locomotor activity.

Backflipping was performed in a rhythmic sequential pattern by all subjects. Performance did not vary so much in rate (eg number of backflips min^{-1}) as in the number of bouts performed. This may be due to the relatively high amount of energy required to sustain the behaviour and the muscular fatigue necessitating frequent rest periods. Subjects would frequently perform a bout of backflips and then remain inactive for 20–40 s before resuming activity. This phenomenon extended to the hourly performance levels as well. For example, the subject represented by the solid black bars in Figure 1 performed at high rates for the first 3h (2000–2300h), became inactive between 2300h and 0000h, and then resumed performance during the 0000–0100h interval. Fatigue may also explain why the average number of backflips bout^{-1} was not greater (overall mean of 7.0) relative to the total number of bouts performed during each 24h period.

Performance levels of stereotyped backflipping in the present study were very high for some individuals. High performance rates of repetitive stereotyped behaviours have been observed in other species such as bank voles (Odberg 1986) and pigs (Rushen 1984; Cronin *et al* 1986). Rushen *et al* (1993) suggested that performance of the behaviour itself may provide positive feedback to the animal even when it is unable to reach the consummatory phase of the behaviour due to environmental constraints. While this is an appealing hypothesis, it is difficult to test since it is often difficult to identify the consummatory experience.

Mason (1993) reported that female mink performed more repetitions of stereotyped locomotor behaviour than males, whereas Odberg (1986) found no gender differences in the frequency of repetitive jumping behaviour in bank voles. In the present study, performance levels of females were higher than those of males but the differences were not statistically significant (Table 1).

Performance was highly cyclical in all subjects, with more than 90 per cent of all stereotypy performance occurring during the hours of darkness. This result is not surprising if one considers that roof rats are nocturnal.

The consistent performance of individuals over consecutive nights validated the use of a single night's data in describing the performance of individuals at a given state of maturation. The consistency in performance of individuals at 30 and 60 days of age provided no evidence for maturation-related changes in performance or for habituation or sensitization of the response during this 1 month period. Of course, the subjects were still relatively young at 60 days of age. Changes in performance might have been observed if the animals had been monitored over a period longer than 30 days. Mason (1993) found the form and timing of repetitive stereotyped behaviour in young mink to be more variable than in older animals. Young mink often performed a variety of repetitive locomotor behaviours, while older mink exhibited only some of these behaviours and usually at feeding time.

Total numbers of backflips performed by cagemates (ie littermates) were positively correlated. Greater resemblance between relatives than between non-relatives provides support to the argument that there was a familial component to the performance of repetitive backflipping in this population of roof rats. However, demonstrating a litter effect on performance does not allow us to conclude that there is a genetic basis for the differences in performance between litters. Maternal effects (common mother) and social facilitation (influence of cagemates) could also explain this difference. The data obtained in the present experiment do not distinguish between heredity and maternal effects.

Less variation in performance was found between sibs within litters compared to unrelated rats (ie between litters). Within-litter standard errors were considerably lower than values obtained in other experiments in this study. There was no evidence that the performance of one individual physically interfered with the performance of its cagemate.

Strain differences in the expression of repetitive locomotor behaviours have been observed in mice (Wurbel *et al* 1996). However, Wurbel and Stauffacher (1996, 1997) found no correlation between mouse cagemates in the performance of a stereotyped behaviour. Social facilitation of repetitive stereotyped behaviours has been reported in some species such as pigs (Appleby *et al* 1989) and voles (Cooper & Nicol 1994). In the present study, the fact that performance levels of littermates housed in different cages were highly correlated argues that familial relationships are more important than social facilitation in the expression of repetitive backflipping behaviour in this species.

Although it seemed appropriate to house subjects in cages with shelters from birth, preliminary studies demonstrated that young reared in such cages still performed stereotyped backflipping after weaning if they were placed in cages without shelters. Thus, provision of a shelter from birth was not incorporated into this experiment.

The mean performance of the shelter-housed subjects was considerably lower than that of all other groups reported in this paper, including their littermate sisters who served as controls. These results are consistent with the hypothesis that shelters can insulate captive rodents from fear-evoking stimuli that may otherwise contribute to the development and expression of repetitive stereotyped behaviours when avoidance responses are thwarted. In nature, rodents survive by being sensitive to changes in their environment (eg predators, aggressive

conspecifics, poison baits, etc). Being able to quickly reach a relatively high state of arousal (ie fearfulness) is adaptive. However, chronic states of high arousal can be maladaptive. Shelters (burrows, etc) not only protect rodents from the elements and predators but may also buffer them from fear- and arousal-provoking extraneous stimulation.

The similarity in performance of male and female rats in experiment 1b was sufficient to justify using females as controls for the male experimental animals in experiment 2. While this decision reduced the total number of animals reared for these experiments, it did not negate the possibility that the shelter could have a different effect on male and female roof rats.

Introducing wooden boxes into the animals' cages provided a stimulus for the test subjects to engage in other activities such as gnawing and nest building. Although these activities were not quantified, they may have provided a substitute activity for backflipping.

Since the roof rat is an active arboreal species, it might be that the repetitive backflipping behaviour observed developed from thwarting the species' natural tendency to climb either for its own sake (ie exploration) or in the context of avoiding fear-inducing stimuli. The outcomes of studies designed to show the relationship between cage size and the development and expression of repetitive stereotyped behaviours have been contradictory and difficult to interpret (Wiedenmayer 1996). In the present study, increasing the amount of vertical wall space eliminated the expression of vertical backflipping at 30 days of age when controls maintained in 'unenriched' cages were consistently exhibiting the behaviour. However, increasing cage height prompted the development of a similar, horizontal circling behaviour that was not seen in standard cages. The height of the enclosure affected the rate of development and form of the roof rats' backflipping behaviour, suggesting a degree of plasticity in the performance of such behaviours. It appears that the expression of backflipping is influenced by environmental quality and that its schedule for development is not rigid.

Although the enhanced natural climbing behaviours permitted by increased cage height may have retarded the development of backflipping behaviour, an alternative hypothesis is that the increased vertical distance from floor to ceiling in the enlarged cages may have discouraged the rats from jumping from ceiling to floor and exhibiting other repetitive locomotor behaviours in a vertical plane. The fact that the subjects eventually developed a similar circling behaviour (albeit horizontally-oriented) suggests that the factors motivating repetitive locomotor behaviours had not been suppressed.

Experiments 2 and 3 demonstrated that providing a shelter or changing the physical configuration of the animal's cage could inhibit the development and expression of stereotyped backflipping. However, it is important to note that neither shelter nor increased cage height totally eliminated this behaviour. Perhaps more extreme modifications of the subjects' environment (eg provision of burrows or much larger enclosures) would have eliminated the behaviour entirely. Sorensen and Randrup (1986) found that enriching the cages of laboratory-reared bank voles with tunnel systems, nest material, hiding places, nuts, etc greatly reduced the incidence of repetitive stereotyped behaviours.

The wild-caught parents of the rats used in this study did not develop backflipping behaviour. Both Sorensen and Randrup (1986) and Cooper and Nicol (1996) noted that wild-caught bank voles did not develop stereotypies in barren laboratory cages while their laboratory-reared counterparts (offspring in some cases) did. It is possible but unlikely that in the present study the relatively low cage ceiling inhibited these larger adults. Interestingly, when the wild-caught adults were startled, they typically responded by freezing rather than by exhibiting active escape behaviours. Being reared in a relatively large outdoor enclosure provided these wild-caught animals with shelter and considerable space for locomotor activity early in life. Also, they were

weaned naturally rather than artificially. Therefore, it is unlikely that they experienced the thwarted suckling motivation discussed by Wurbel and Stauffacher (1997) as a factor that may contribute to the development of repetitive stereotyped behaviours in laboratory-reared rodents.

The development of backflipping and similar jumping stereotypies in captive rodents does not appear to be confined to arboreal species. Fossorial rodents such as bank voles, hamsters and grasshopper mice (*Onychomys torridus*) often develop these same behaviours. Mason (1993) reported that mink would occasionally develop somersaulting stereotypies.

The results of this study are consistent with the hypothesis that the performance of repetitive stereotyped behaviour by captive rodents may be linked to heightened states of arousal (Berkson & Mason 1964). Such behaviours may lower the performer's arousal (ie regulate it) or they may simply be indicators of heightened arousal (Keiper 1969; Hutt & Hutt 1970). Hence, it is not known if the performance of repetitive backflipping by roof rats benefits the performers by somehow moderating the arousing effects of their environment.

Animal welfare implications

Captive rodents are typically maintained in small laboratory cages with relatively little opportunity for perceptual and locomotor stimulation. In addition, captive rodents are artificially weaned at an earlier stage of development than would occur naturally. Being subjected to early weaning and placed in a relatively impoverished environment can encourage the development of repetitive stereotyped locomotor behaviours such as the backflipping described in this paper. The incidence and intensity of the repetitive behaviours exhibited may vary depending on the size and configuration of the cage, the presence or absence of shelter and the familial and evolutionary background of the animals involved. Weaning management in young rodents, cage design and genetic selection are areas with great potential for improving the welfare of captive rodents.

We have used the term 'stereotyped' sparingly in this report to avoid the inference that repetitive backflipping in captive roof rats reflects a negative mental state or that the animals' welfare is jeopardized by such behaviours. While such assumptions could be true, it is also possible that backflipping facilitates adaptation to a relatively impoverished environment. The present study provides no evidence to support or refute such claims.

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