Effect of early nutritional experience on the feeding behaviour of adult female rats

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ABSTRACT: In the present paper the effect of postnatal undernutrition on feeding behaviour has been evaluated in mature female Wistar rats subjected to food restriction a) during the suckling period, i. e. up to day 15 (SR), b) during the weaning period from day 15 to 30 (WR), c) throughout 30 days post partum (SWR) and d) during adulthood, i. e. from day 60–75 of life (AR). In comparison with the *ad libitum* fed controls (C), the lactating mothers and the pups of the food-restricted groups were allowed free access to food for only two hours daily. In experimental groups this restriction was then changed to an *ad libitum* regime. On day 90 food intake was evaluated daily in five 20 min lasting sessions after 23 h of fasting in group-housed and single-housed rats exposed to their home as well as to their experimental environment. The significantly decreased body weight found on day 30 and 90 in females coming from litters of restrictedly fed mothers, as compared with those fed *ad libitum*, showed that these animals were considerably undernourished. Appetitive motivation increased in those groups of females that had been exposed to a restricted feeding regime during their infant period but remained unaffected in females restrictedly fed during their adult age. In comparison with the *ad libitum* fed controls and AR groups, significantly increased mean food intake was observed in all postnatally underfed groups ($P < 0.001$). The greatest inclination to hyperphagia and qualitative changes in feeding behaviour were observed in SWR females whose feeding regime was restricted for the longest time, i. e. during the suckling and the weaning period, as compared to groups with shorter food restriction. These animals showed hyperphagia even in the new environment regardless whether the whole group or only one female was tested. Our results reveal a) a determinant influence of the feeding regime of the animals at early age (41%) while environmental and social factors represent only about 17% and 4%, respectively and that b) changes in feeding habits in adult female rats may significantly depend on the length of postnatal undernutrition.

Keywords: postnatal undernutrition; food intake; environmental and social effects; female rats

Feeding behaviour in socially living species can be affected by manipulation of their environment. Extensive experimental data related to stressful or aversive influences on food consumption demonstrated that tail pinch (Greeno and Wing, 1994), repeated cold stress (Kawanishi *et al.*, 1997; Schultz *et al.*, 1999) subsequently promote feeding while electrical shocks (Rickards *et al.*, 1997), chronic noise (Alario *et al.,* 1987) and restraint (Grignaschi *et al.*, 1993; Zylan and Brown, 1996) decreased food intake in rodents. In addition to these influences the social and environmental factors and their complicated interactions also appear to be important in the mechanism of the onset of eating disorders. For instance, Ewer (1968) demonstrated social depression and decreased feeding for rats and mice in group-housing conditions in contrast to individually housed animals. Galef (1992) and Pérez *et al.* (1997) observed increased food intake in individually housed rats, in contrast to animals housed in groups. However, the role of housing in the development of feeding disorders is controversial. While moving the rats from individual to pair housing results in decreased food uptake for a few days (O'Connor and Eikelboom, 2000), re-housing of the rats from pair to individual housing has no effect on either food consumption or body weight. It has also been stated that feeding suppression is

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related rather to changed housing than to novelty of the partner (Lopak and Eikelboom, 2000). Moreover, it was also demonstrated that isolation decreased habituation to a novel environment (Einon *et al.*, 1975) and that singly housed rats in comparison with socially housed animals exhibited increased environmental neophobia under open-field conditions and prolonged latencies to contact and eat food (Holson, 1986; Hall *et al.*, 1997). There are however other studies showing food consumption to be differently affected in dependence upon the time when the period of individual housing was induced. When isolated housing of the rats began at the weaning period, their food consumption and body weight increased (Fiala *et al.*, 1977), on the other hand, isolation after weaning resulted in decreased feeding (Goodrick, 1974; Yamada *et al.*, 2000). On the whole, these reports suggest that changed environmental and social experience may be associated with appetitive disorders to some extent; however, there is no general agreement on the way in which this experience influences development of feeding behaviour.

The conditions under which animals are reared and housed are a crucial determinant of their growth and food intake. During the early life period the rat pups show increased sensitivity to different environmental stimuli, particularly to insufficient nutrition of their mothers. When such insufficient nutrition occurred in young rats within the first three weeks of life, their body weight was negatively affected not only during the lactation period (Boxwel *et al.,* 1995) but also after weaning despite of subsequent nutritional rehabilitation (Bartness *et al.*, 1987). In addition to decreased body growth another consequence of undernutrition during this "critical" life period in rats may also be the change in their food intake during adulthood. Male rats underfed throughout lactation by feeding their mothers with a restricted quantity of food proved to eat more during adulthood as compared with the well-fed controls (Smart and Dobbing, 1977). On the other hand, a daily 6 h separation of the mother during lactation which affects the normal mother-infant interaction did not change the food intake of female rats under standard feeding conditions in later life. However, using the method of a 2 h time-restricted scheduled feeding some authors observed enhanced food consumption in these animals at the age of 6 and 9 weeks (Iwasaki *et al.*, 2000). These studies indicate that behavioural observations incorporate more information about the contribution of early life events to ingestive disorders than any other simple parameters such as mean daily food intake and body weight.

However, the association of feeding behaviour in later life with early undernutrition has not been examined extensively yet. The present study was therefore designed to provide information on the effects of early undernutrition on feeding behaviour in later life. In these experiments our animal model of undernutrition was employed using a restricted feeding regime at strictly defined developmental stages. In adult female rats undernourished either during suckling, weaning, in both periods or during adulthood, food consumption was examined in socially and singly housed animals in both home and in experimental environments.

MATERIAL AND METHODS

Animals

Experiments were performed on first-time lactating Wistar rat dams. On the first day after birth the litters were adjusted to 8 pups per nest with equal numbers of females and males if possible. The litters were individually housed in small (0.42 m × 0.27 m × 0.22 m) plexiglass cages in a temperature-controlled environment 21 ± 1°C with a 12L : 12D regime (light from 6:00–18:00 h). The standard pellet diet DOS 2b (Velaz Prague) and tap water was at their disposal except when food restriction was applied. After weaning on day 30 the male rats were excluded from the experiment and the female rats were housed by five in large (0.56 m × 0.35 m × 0.19 m) plexiglass cages.

Food restriction at a strictly defined developmental stage was adjusted so that lactating females and their offspring had free access to food for only two hours daily (from 8:00–10:00). The mothers were fed daily a good quality diet at approximately 50% of the amount eaten by the control mothers fed *ad libitum*. The following groups were used in the experiment:

C (control females with constant free access to food and water)

SR (animals food-restricted during the suckling period, i. e. up to day 15 of life)

WR (restrictedly fed rats during the weaning period, between day 15–30 of life)

SWR (animals food-restricted from birth to weaning)

AR (rats restrictedly fed in their adulthood, i. e. from day 60–75 of life).

Body weight measurements were taken at 2, 30 and 90 days of age in all groups as indicated in Table 1.

Apparatus and procedure

The home environment was constructed by connecting two standard laboratory cages via a 0.15 m long tunnel of 0.1 m in diameter. The unfamiliar environment was ensured by a specially constructed novodur cage sized 0.7 m × 0.7 m × 0.7 m. A 0.1 m high cone, 0.3 m in diameter, with a circular platform of 0.05 m in diameter was placed in its centre. The feeding behaviour was investigated in 90 day-old animals. 10 females with the same restricted feeding regime were tested in the home environment first as a group and then individually. 10 females with the same feeding regime were examined in an unfamiliar environment (first as a group and then individually). Food intake of the rats under different social and environmental conditions was compared. The rats were recognised by an ink mark on the tail.

Prior to the experiments the animals were allowed a preparatory stage of five days. During this period the rats were fed only one hour daily but had *ad libitum* access to water. The food sample prepared from the standard laboratory diet DOS 2b (Velaz Prague) by addition of water, was placed for one hour into both home and unfamiliar cages and then removed. On the day of the experiment (after 23 hours of fasting) the animals received 1 gram weighing food pellets prepared every day 1 hour before starting the experiment from the standard minced laboratory diet DOS 2b (Velaz Prague) which was liquefied by the addition of 50% water. The pellets were given to the rats one by one in their home cage or on the platform of their unfamiliar cage. For individual rats there was always one food pellet at disposal. The number of food pellets eaten by each female was recorded. The experiment was started first with the observation of the group-housed females and then continued the following week with the examination of individually-housed rats. The animals were evaluated daily in five sessions, each day one. Observation was started in the morning hours (from 8:00–10:00) and lasted 20 minutes.

Body weight and food consumption was analysed using one-way analysis of variance (ANOVA). The significance of differences between the means was calculated by Tukey's test. The influence of food restriction on food intake under different environmental and social conditions was analysed using a three-way analysis of variance ANOVA

RESULTS

Different feeding regimes of rat dams significantly influenced the body weight of the pups. The pups coming from litters of restrictedly fed dams (SR, WR, SWR), as compared with the pups of the

Table 1. Mean body weight of control and restrictedly fed females (g/female)

Group	Day 2	Day 30	Day 90
C	6.4 ± 0.1	101.0 ± 1.7	301.0 ± 2.5
SR	6.5 ± 0.1	58.2 ± 0.7*	208.7 ± 2.6*
WR	6.3 ± 0.1	57.2 ± 0.8*	236.9 ± 2.8*
SWR	6.3 ± 0.1	32.5 ± 0.8*	219.3 ± 1.6*
AR	6.3 ± 0.1	102.3 ± 1.6	224.0 ± 2.7*
$P <$	NS	0.001	0.001

The values are means ± S.E.M.; the results were evaluated by one-way ANOVA
*difference statistically significant as compared with the control (C)

dams fed *ad libitum* (C, AR), showed significantly lower body weight on day 30. At that time the body weight of postnatally underfed rats was lower by about 42–70% than that of the controls. Despite of nutritional rehabilitation the body weight of all restrictedly fed groups was significantly lower (25–30%) on day 90 than that observed in the *ad libitum* fed controls (Table 1).

Table 2 shows the mean food intake values (5 experimental sessions each lasting 20 min) in the undernourished and control groups under different environmental and social conditions. While in the group-housed controls (C) as compared with single-housed animals food intake in the home environment was significantly increased and the phenomenon of social facilitation elicited, unfamiliar environmental conditions had an opposite effect, i.e. group-housed rats revealed decreased food intake and the phenomenon of social depression was observed ($F = 33.2$, $P < 0.001$) (Table 2). Postnatally underfed SR females appeared to eat significantly more in the home than in the unfamiliar environment. While no change in food intake was observed in the home cage rats under different social conditions, the animals housed in groups in an unfamiliar cage showed higher food intake and the phenomenon of social facilitation could be demonstrated in comparison with individually housed rats ($F = 31.2$, $P < 0.001$) (Table 2). The evaluation of food intake in WR groups revealed that in the home environment group-housed females consumed less food than individually housed females and the phenomenon of social depression was observed. On the other hand, in animals housed in unfamiliar cages food intake was similar under different social conditions ($F = 19.1$, $P < 0.001$) (Table 2). In comparison with the SR and WR groups food intake of the SWR females did not significantly change either under new environmental or under different social conditions ($F = 0.4$, NS) (Table 2). Of rats restrictedly fed during adulthood (AR group) very low food consumption was typical in all experimental situations. No change in food consumption was seen in home cage-housed rats under different social conditions. Moreover, in comparison with the individually housed animals the group-housed rats appeared to eat significantly less in the unfamiliar environment and the phenomenon of social depression was observed ($F = 7.2$, $P < 0.001$) (Table 2).

Analysis of food intake for each group in all experimental situations revealed a significant increase in the mean values in postnatally underfed rats, i. e. 19.0 ± 0.9, 22.8 ± 0.8, 24.8 ± 0.9 in SR, WR, SWR groups, respectively, as compared with the control (13.0 ± 0.8) and AR group (11.3 ± 0.8) ($F = 50.3$, $P < 0.001$). The results showed not only interaction between the nutritional regime and environmental conditions ($F = 15.2$, $P < 0.001$) but also interaction between the nutritional regime and social conditions ($F = 10.3$, $P < 0.001$). The interaction between the environmental and social conditions was not significant ($F = 2.2$, NS). Three-way ANOVA revealed a significant interaction between the nutritional regime, environmental and social conditions ($F = 23.8$, $P < 0.001$). From among the mentioned factors affecting food intake the nutritional regime, the environmental and social effects account for 41%, 17% and 4%, respectively. The other effects were not examined in the experiment.

Table 2. Mean food intake (number of pellets)

Group	Home group-housed session	Home singly-housed session	Unfamiliar group-housed session	Unfamiliar singly-housed session	F_1	$P <$
C	18.1 ± 1.4	6.0 ± 0.6	7.3 ± 1.2	20.6 ± 1.7	33.2	0.001
SR	27.0 ± 1.6	24.6 ± 1.1	16.3 ± 1.9	8.0 ± 1.4	31.2	0.001
WR	17.6 ± 1.8	31.3 ± 0.6	21.0 ± 1.5	21.3 ± 1.1	19.1	0.001
SWR	26.2 ± 1.6	24.6 ± 1.0	24.7 ± 2.6	23.5 ± 1.5	0.4	NS
AR	12.6 ± 1.9	15.2 ± 1.4	5.8 ± 1.1	11.7 ± 1.3	7.2	0.001

The values are means ± S.E.M. from sessions 1–5; the results were evaluated by one-way ANOVA

DISCUSSION

In the present experiment decreased body weight was observed in pups coming from the nests of restrictedly fed mothers, which is in agreement with the data reported by other authors (Babický and Nováková, 1986; Campbell and Bedi, 1989; Almeida *et al.*, 1992; Boxwell *et al.,* 1995; Loranca *et al.*, 1999). The observed growth stunting was more pronounced in animals restrictedly fed during 30 days post partum (SWR group) than in both groups with a shorter period of food restriction. Moreover, all previously underfed rats remained lighter in adulthood than the *ad libitum* fed controls despite of food rehabilitation, which suggests that postnatal undernutrition induces serious effects on feeding habits during the early and late life periods.

Milk is the only source of water and food for the rat pups until 15–16 days after birth (Babický *et al.,* 1972) and their intake gradually increases from birth until day 15–20 in *ad libitum* fed mothers (Babický *et al.*, 1970, 1973; Fiorotto *et al.,* 1991). On the other hand, milk production of the rat dams is altered by chronic dietary restriction which in turn may affect the growth of their pups. It was demonstrated that food restriction throughout lactation reduced the milk yield, growing pups utilising milk energy less efficiently and being smaller than those nursed by *ad libitum* fed dams (Rasmussen and Warman, 1983; Young and Rasmussen, 1985; Sadurskis *et al.*, 1991; Boxwel *et al.,* 1995). Moreover, almost twofold increased milk fat and substantially increased milk protein concentration was recorded in restrictedly fed dams (Mozeš *et al.,* 2000), which indicates a proportionally decreased water content in their milk. In relation to that our experiment revealed the characteristic feature of thin-looking skin and a generally dehydrated appearance of 2 and 3 day-old undernourished pups. It is not clear, however, if the later growth and behavioural changes in postnatally underfed rats could be caused by decreased intake of water or food or both during the suckling period. It is well known that food intake is closely related to water intake and vice versa. While food restriction reduced water intake (Bellingham *et al.*, 1986) restriction of water resulted in lower food consumption (Levitsky, 1970).

Undernutrition of lactating females produces not only a decreased amount of milk available to the pups but also changes in the mother-litter behaviour (Fraňková, 1971; Smart and Preece, 1973; Crnic, 1976). The pups coming from litters of restrictedly fed mothers are underfed, smaller, less mature and emit fewer ultrasonic calls (Hunt *et al.*, 1976). The food-deprived mothers showed a longer period of exploratory behaviour and needed a longer time to retrieve their pups as compared with the well-fed mothers (Massaro *et al.,* 1974). As proved by delayed ear and eye opening (Salas *et al.,* 1991) the sensorial system is particularly sensitive to perinatal undernutrition. The central nervous system of neonatal rats is considered to be immature in almost all aspects. The suckling period appeared to be a critical one significantly influencing the functional activity of the hypothalamic structure, amygdala, hippocampus and nucleus accumbens (Mozeš *et al.,* 1991; Maldonado-Irizarry *et al.,* 1995; Elmquist *et al.,* 1999; Stratford and Kelly, 1999) which are closely involved in motivational and food intake behaviour. From this point of view decreased food-water intake of rat pups may permanently influence the development of both growth and food intake regulation mechanisms while a restricted feeding regime introduced at adulthood probably affects only the growth of animals. Evaluation of feeding behaviour under different experimental conditions revealed that SR rats (restrictedly fed during the suckling period) consumed significantly less food in a new (unfamiliar) environment than in the home environment. Moreover, in comparison with the group-housed animals, food intake was suppressed during individual sessions and social facilitation was observed. These results are to some extent similar to those found in re-housed rats in which food intake was suppressed in the new environment, even though fed with familiar food (Holson, 1986). These rats are not fully able to eat familiar food in a new environment since a new cage might be a stressing factor. This reluctance has been labelled as "feeding neophobia" and is related to avoidance of predators and traps. On the other hand, food intake in SWR females (restrictedly fed during the suckling and weaning period) did not significantly differ in a new environment under different social conditions, suggesting that these rats might not have acquired a normal feeding behaviour. As noted previously, decreased feeding and social depression were found in group-housed rats and mice in contrast to singly-housed animals (Ewer, 1968; Fiala *et al.,* 1977; Pérez *et al.,* 1997). Our experiment, however, proved this fact not to be a phenomenon that would be stable for the given population. This

phenomenon was not found in SWR rats while in WR and AR subjects social depression, in SR rats social facilitation and in C females the combination of these phenomena was observed. Our results indicate that it is a variable and situation-dependent phenomenon which may be changed by early nutritional experience. It is also well known (Cabanac and Swiergiel, 1989) that both food deprivation and chronic food restriction increases food hoarding of laboratory rats. Additionally, in our previously underfed females increased food hoarding was observed under individual-housing conditions in both home and experimental environments, which suggests a profound late effect of undernutrition on the feeding habits of these animals (unpublished observation).

In comparison with the *ad libitum* fed controls and females restrictedly fed during adulthood a substantial increase in mean food consumption was observed in all three postnatally underfed groups. In comparison with C and AR rats (13.0 ± 0.8 vs. 11.3 ± 0.8), about twice as high food consumption was found in SWR rats (24.8 ± 0.9) while the food intake of WR females tended to be higher than in the SR group (22.8 ± 0.8 vs. 19.0 ± 0.9). These results seem consistent with the high prevalence of undernutrition induced by eating disorders observed in adult females. Evaluation of all three factors (nutritional, environmental and social components) proved the nutritional regime (41%) to be the most expressive determinant affecting food intake in later life while the environmental and social factors account for only about 17% and 4%, respectively.

Analysis of the feeding behaviour studied in the present experiment has provided information about the relation between early feeding experience and food consumption changes in adult female rats. Distinct behavioural changes and also significantly increased food intake were observed in these rats in different housing conditions. The most expressive changes were seen in females restrictedly fed from birth to weaning as compared to groups with a shorter food restriction period. From this point of view changes in the feeding habits of adult females may significantly depend on the duration of postnatal undernutrition.

REFERENCES

Alario P., Gamallo A., Beato M.J., Trancho G. (1987): Body weight gain, food intake and adrenal development in chronic noise stressed rats. Physiol. Behav., *40*, 29–32.

Almeida S.S., Soares E.G., Bichuette M.Z., Graeff F.G., De Oliveira L.M. (1992): Effects of early postnatal malnutrition and chlordiazepoxide on experimental aversive situations. Physiol. Behav., *51,* 1195–1199.

Babický A., Nováková V. (1986): Protein malnutrition of the lactating female rat: Effect on maternal behaviour and spontaneous weaning of young rats. Physiol. Bohemoslov., *35,* 456–463.

Babický A., Ošťádalová I., Pařízek J., Kolář J., Bíbr B. (1970): Use of radioisotope technique for determining the weaning period in experimental animals. Physiol. Bohemoslov., *19,* 457–467.

Babický A., Pavlík L., Pařízek J., Ošťádalová I., Kolář J. (1972): Determination of the onset of spontaneous water intake in infant rats. Physiol. Bohemoslov., *21,* 467–471.

Babický A., Ošťádalová I., Pařízek J., Kolář J., Bíbr B. (1973): Onset and duration of the physiological weaning period for infant rats reared in nests of different size. Physiol. Bohemoslov., *22,* 449–456.

Bartness T.J., Goodlett Ch.R., Morgane P.J. (1987): Effects of pre- and early postnatal protein malnutrition on carcass composition and lipoprotein lipase activity in male rats. Physiol. Behav., *39,* 721–726.

Bellingham G.K., Bellingham W.P., Storlien L.H. (1986): Effects of scheduled food and water deprivation on food intake, water intake and body weight of cage-adapted and cage-naive rats. Appettite, *7,* 19–39.

Boxwell J., Ayson P., Ramenofsky M. (1995): Growth and metabolic parameters in pups of undernourished lactating rats. Physiol. Behav., *57,* 469–475.

Cabanac M., Swiergiel A.H. (1989): Rats eating and hoarding as a function of body weight and cost of foraging. Am. J. Physiol., *257,* R 952–957.

Campbell L.F., Bedi K.S. (1989): The effects of undernutrition during early life on spatial learning. Physiol. Behav., *45,* 883–890.

Crnic L.S. (1976): Maternal behavior in the undernourished rat (*Rattus norvegicus*). Physiol. Behav., *16,* 677–680.

Einon D., Morgan M.J., Sahakian B.J. (1975): The development of intersession habituation and emergence in socially reared and isolated rats. Dev. Psychobiol., *8,* 553–559.

Elmquist J.K., Elias C.F., Saper C.B. (1999): From lesions to leptin: hypothalamic control of food intake and body weight. Neuron, *22,* 221–232.

Ewer R.F. (1968): Ethology of Mammals. Logos Press, London. 273 pp.

Fiala B., Snow F.M., Greenough W.T. (1977): "Impoverished" rats weight more than "enriched" rats because they eat more. Dev. Psychobiol., *10,* 537–541.

Fiorotto M.L., Burrin D.G., Perez M., Reeds P.J. (1991): Intake and use of milk nutrients by rat pups suckled in small, medium, or large litters. Am. J. Physiol., *260,* R 1104–1113.

Fraňková S. (1971): Relationship between nutrition during lactation and maternal behaviour of rats'. Activ. Nerv. Super., Prague, *13,* 1–8.

Galef B.G. Jr (1992): Weaning from mothers milk to solid foods. The developmental psychobiology of self-selection of foods by rats. Ann. NY Acad. Sci., *662,* 37–52.

Goodrick C.L. (1974): The effect of protein malnourishment and caging on growth and behavior of laboratory mice. Dev. Psychobiol., *7,* 249–256.

Greeno C.G., Wing R.R. (1994): Stress-induced eating. Psychol. Bull., *115,* 444–464.

Grignaschi G., Mantelli B., Samanin R. (1993): The hypophagic effect of restraint stress in rats can be mediated by 5-HT2 receptors in the paraventricular nucleus of the hypothalamus. Neurosci. Lett., *152,* 103–106.

Hall F.S., Humby T., Wilkinson L.S., Robbins T.W. (1997): The effects of isolation-rearing of rats on behavioral responses to food and environmental novelty. Physiol. Behav., *62,* 281–290.

Holson R.R. (1986): Feeding neophobia: A possible explanation for the differential maze performance of rats reared in enriched or isolated environments. Physiol. Behav., *38,* 191–201.

Hunt L.E., Smotherman W.P., Wiener S.G., Levine S. (1976): Nutritional variables and their effect on the development of ultrasonic vocalisations in rat pups. Physiol. Behav., *17,* 1031–1039.

Iwasaki S., Inoue K., Kiriike N., Hikiji K. (2000): Effect of maternal separation on feeding behavior of rats in later life. Physiol. Behav., *70,* 551–556.

Kawanishi C., Fukuda M., Tamura R., Nishijo H., Ono T. (1997): Effects of repeated cold stress on feeding, avoidance behavior, and pain-related nerve fibre activity. Physiol. Behav., *62,* 849–855.

Levitsky D.A. (1970): Feeding patterns of rats in response to fasts and changes in environmental conditions. Physiol. Behav., *5,* 291–300,

Lopak V., Eikelboom R. (2000): Pair housing induced feeding suppression: individual housing not novelty. Physiol. Behav., *71,* 329–333.

Loranca A., Torrero C., Salas M. (1999): Development of play behavior in neonatally undernourished rats. Physiol. Behav., *66,* 3–10.

Maldonado-Irizarry C.S., Swanson C.J., Kelley A.E. (1995): Glutamate receptors in the nucleus accumbens shell control feeding behavior via the lateral hypothalamus. J. Neurosci., *15,* 6779–6788.

Massaro T.F., Levitsky D.A., Barnes R.H. (1974): Protein malnutrition in the rat: its effects on maternal behavior and pup development. Dev. Psychobiol., *7,* 551–561.

Mozeš Š., Lenhardt Ľ., Raček Ľ. (2000): Milk composition in restrictedly fed rats. Vet. Med. – Czech, *45,* 141–144.

Mozeš Š., Kuchár S., Michalov M., Nováková V. (1991): Influence of litter size on the RNA content of VMH and LHA in preweaning rats. Physiol. Behav., *50,* 1133–1136.

O'Connor R., Eikelboom R. (2000): The effects of changes in housing on feeding and wheel running. Physiol. Behav., *68,* 361–371.

Pérez C., Canal J.R., Domínguez E., Campillo J.E., Guillén M., Torres M.D. (1997): Individual housing influences certain biochemical parameters in the rat. Lab. Anim., *31,* 357–361.

Rasmussen K.M., Warman N.L. (1983): Effect of maternal malnutrition during reproductive cycle on growth and nutritional status of suckling rat pups. Am. J. Clin. Nutr., *38,* 77–83.

Rickards S.L., Job R.F.S., Boakes R.A. (1997): Effects of acute shock on body weight are mediated by changes in food intake. Anim. Learn. Behav., *25,* 437–445.

Sadurskis A., Sohlstrom A., Kabir N., Forsu E. (1991): Energy restriction and the partitioning of energy among the costs of reproduction in rats in relation to growth of the progeny. J. Nutr., *121,* 1798–1810.

Salas M., Pulido S., Torrero C., Escobar C. (1991): Neonatal undernutrition and self-grooming development in the rat: Long-term effects. Physiol. Behav. *50,* 567–572.

Schultz L.A., Collier G., Johnson D.F. (1999): Behavioral strategies in the cold: Effects of feeding and nesting costs. Physiol. Behav., *67,* 107–115.

Smart J.L., Preece J. (1973): Maternal behaviour of undernourished mother rats'. Anim. Behav., *21,* 613–619.

Smart J.L., Dobbing J. (1977): Increased thirst and hunger in adult rats undernourished as infants: an alternative explanation. Brit. J. Nutr., *37,* 421–430.

Stratford T.R., Kelley A.E. (1999): Evidence of a functional relationship between the nucleus accumbens shell and lateral hypothalamus subserving the control of feeding behavior. J. Neurosci., *19,* 11040–11048.

Yamada K., Ohki-Hamazaki H., Wada K. (2000): Differential effects of social isolation upon body weight, food consumption, and responsiveness to novel and social environment in bombesin receptor subtype-3 (BRS-3) deficient mice. Physiol. Behav., *68,* 555–561.

Young C.M., Rasmussen K.M. (1985): Effects of varying degrees of chronic dietary restriction in rat dams on reproductive and lactational performance and body composition in dams and their pups. Am. J. Clin. Nutr., *41,* 979–987.

Zylan K.D., Brown S.D. (1996): Effect of stress and food variety on food intake in male and female rats. Physiol. Behav., *59*, 165–169.

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