
Observations on the prevalence of nest-building in non-breeding TO strain mice and their use of two nesting materials

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Summary

The spontaneous performance of nest-building behaviour by non-breeding laboratory mice suggests that routinely providing nesting material might be a suitable environmental enrichment. If nesting material is to be provided routinely, this should have characteristics which are preferred, or at least accepted by a considerable proportion of the animal population; it should also be inexpensive. The present study therefore examined the prevalence of nest-building behaviour in 39 individually-housed, non-breeding, female mice, and their preferences for a commercial nesting product and a less expensive source of material (paper towels). Within minutes of the materials being placed in the cages, the mice began manipulating the paper towels. Thirty-six of the mice subsequently constructed nests during the first dark phase after the materials had been placed in the cage — the remaining three mice constructed nests during the following 48 h. The nests were usually constructed from a mixture of the two materials, though observations indicated the mice might have preferred characteristics of the inexpensive paper towels. There was a strong tendency to build nests in the same location used for sleeping prior to the nesting material being provided, and similarly, the mice were conservative in the site chosen to build a second nest after the first was removed. The most frequently chosen site for nest-building was under the feeder. Other studies have reported a high motivation for nest-building behaviour, widespread performance amongst many strains, and nest-building as a thermoregulatory behaviour by animals housed in standard laboratory air temperature. In conjunction with these findings, the present results suggest that routinely providing paper towels is an inexpensive and practical means of environmental enrichment for non-breeding, laboratory mice.

Keywords Environmental enrichment; mice; nesting behaviour; preferences; welfare

It has been argued that to ensure good welfare, the husbandry of captive animals should allow them freedom to perform most 'normal' behaviours (e.g. FAWC 1993), or enable them to perform most behaviours which their progenitors/wild conspecifics exhibit (e.g. Veasey *et al.* 1996). Using this latter approach, Dawkins (1989) reported that Red Junglefowl, the ancestors of modern strains of laying hen, spent 34% of the day scratching and pecking at ground litter whilst

searching for feed. The cage environment of modern layer hens prevents them from performing these behaviours and the occurrence of abnormal, sometimes fatal injurious behaviours have been linked with this shortcoming. It has been reported that wild mice frequently build nests (Van Oortmerssen 1971, Estep *et al.* 1975, Castle & Marshall 1990, Brain 1992) and when materials are provided, inbred strains of laboratory mice build nests of a comparable or slightly larger

size than those built by wild-type counterparts (Estep *et al.* 1975, Lynch 1977). But, although both breeding (Lisk *et al.* 1969, Lisk 1971, Wainwright 1981, Broida & Svare 1983, Schneider & Lynch 1984, Scharmann 1991, Brain 1992) and non-breeding (e.g. Lisk *et al.* 1969, Lisk 1971, Van Oortmerssen 1971, Roper 1973, Scharmann 1991, Brain 1992) laboratory mice build nests when materials are available, nesting materials are usually provided routinely only for breeding females. Therefore, non-breeding mice are commonly housed under conditions which preclude a 'natural' behaviour that is frequently performed by wild-type progenitors. It is possible that such husbandry is sub-optimal with regards to ensuring good welfare.

Nest-building by laboratory mice can be categorized as either maternal or non-maternal. The former has been widely investigated and the effects of environmental (Noirot 1974, Lynch & Possidente 1978, Porter & Busch 1978), genetic (Lynch 1977, Lynch & Possidente 1978, Nee *et al.* 1992) and endocrinological (Voci & Carlson 1973, Lynch & Possidente 1978, Lisk *et al.* 1969, Lisk 1971) factors have been described in detail. Although there are many reports of non-maternal nest-building by mice (e.g. Lee & Wong 1970, Van Oortmerssen 1971, Lee 1973, Roper 1973, Schneider *et al.* 1973, Voci & Carlson 1973, Noirot 1974, Glaser & Lustick 1975, Lynch 1977, 1980, Lynch *et al.* 1986) its occurrence under laboratory conditions has less frequently been the focus of investigation. If it is ascertained that providing nesting materials is advantageous e.g. by promoting natural behaviours, increasing behavioural diversity, or decreasing food intake with no effect on growth (Lacy *et al.* 1978, Stephenson & Malik 1984), it could be argued that we should routinely supply these materials to both breeding and non-breeding animals. But, if provision of such environmental enrichment is to be widely adopted, the desired changes to behaviour or performance of the appropriate activity should be expressed by a large proportion of the population. One aim of this investigation was to examine how prevalent spontaneous nest-building behaviour is amongst non-breeding mice.

When suggesting changes to animal husbandry, it is important to recognize practical constraints. If nesting material is to be routinely supplied to non-breeding animals, it should be readily available, easily handled by technicians and inexpensive. Although commercial nesting materials for pet rodents are available, these are almost certainly prohibitively expensive and can be troublesome to handle. Encouragingly, laboratory mice (Roper 1973 1975abc, Rajendram *et al.* 1987, Blom *et al.* 1993, van de Weerd *et al.* 1994), rats (Bradshaw & Poling 1991) and hamsters (Jansen *et al.* 1969) will build nests from inexpensive paper strips or paper towels. Therefore, the second aim of the present study was to determine whether mice exhibited a preference for an inexpensive source of paper or a more expensive, fibrous material for the construction of nests.

Materials and methods

Thirty-nine virgin, female TO mice bred 10 months previously in the laboratory were housed individually in standard mouse cages measuring 33 × 20 × 19 cm (W × D × H) and containing 1 cm of sawdust. The mice had been reared in single-sex, sibling groups prior to being placed in the experimental cages and had no prior experience of potential nesting materials other than sawdust.

For seven days after the mice were placed in the cages, scans were made (as described below) to determine the site preferred by the mice for sleeping. After the 16:00 h scan on the seventh day, two plastic pots 9 cm high and 10 cm diameter were placed at the rear of each cage. A wad of 100% cellulosic fibre bedding ('Nestle Down', Interpet, Surrey, UK) weighing approximately 4.5 g was placed in the left pot for 20 mice and in the right pot for the remainder. In the other pot was placed a sheet (34 × 20 cm) of 2-ply paper hand-towel ('Hywipes', Bristol Industrial Protections, Bristol, UK) weighing 3.2 g. The pots were retained in a vertical position against the rear wall by metal clips and a small amount of both materials was left remaining visible above the rim of the pot. Scans were continued for the following six days. All

fibrous and paper nesting material was then removed and replenished with fresh material, placed in the pot opposite to that in which it had been supplied previously.

Table 1 The locations preferred by mice for sleeping, prior to nesting materials being placed in the cage

Sleeping location	No. scans	% of scans*	No. mice choosing site as most preferred †
Under feeder	152	34.8	16
Under drinker	118	27.0	10
Rear of cage	72	16.5	6
Other 'Active'	95	21.7	7
TOTAL	628		39

*Including only those scans when a mouse was recorded as sleeping

†Based on the modal frequency recorded for each mouse

Observations were made in the following way. On two or three occasions each day (at 10:00, 13:00 or 16:00 h) the experimental room was entered quietly and each cage scanned. If the mouse was sleeping or was in a nest and had obviously just awoken after being disturbed by the observer, the position of the mouse was noted. If the mouse was in a nest, the materials used in its construction were also noted. During the period prior to nesting material being placed in the cage, the sleeping sites were designated as 'under the feeder', 'under the drinker', 'in the rear third of the cage' or 'other' (i.e. the remainder of the cage). When the pots and nesting materials were present, the location 'rear of the cage' was replaced by 'the pot supplying paper' and 'the pot supplying fibre'. The mouse was recorded as 'active' if it was moving about the cage.

The room lights (100 W incandescent bulbs) were on between 08:00–17:00 h and the ambient temperature was maintained at 21°C with a range of ±1°C.

Table 2 The locations preferred by mice for nest-building, and the materials used in construction of the nest

Nest location	Materials used in nest	No. Scans	% of scans*	No. mice choosing site/material as most preferred †
Under feeder	Mix	368	37.4	15.5
	Paper	39	3.9	2.0
	Fibre	0	0.0	
	None	3	0.3	
Under drinker	Mix	114	11.6	3.0
	Paper	25	2.5	
	Fibre	0	0.0	
	None	15	1.5	
Pot with paper	Mix	97	9.9	4.5
	Paper	34	3.5	2.0
	Fibre	0	0.0	
	None	0	0.0	
Pot with fibre	Mix	89	9.1	5.5
	Paper	0	0.0	
	Fibre	8	0.8	
	None	1	0.1	
Other (main cage)	Mix	186	18.9	7.5
	Paper	2	0.2	
	Fibre	0	0.0	
	None	2	0.2	
'Active'		322		
TOTAL		1305		39

*Including only those scans when a mouse was recorded as sleeping

†Based on the modal frequency recorded for each mouse. When the mouse was equivocal (n=4 mice) its score was shared between the two options it chose most frequently

Results

Prior to the nesting materials being placed in the cages, the majority of mice preferred to sleep under the feeder (Table 1) though several consistently slept in the rear or main sections of the cage which did not provide overhead cover. None of the mice constructed nests with sawdust as described previously (Sherwin 1996a).

Within 2–3 min of the nesting materials being placed in the cages, many mice had pulled the paper towel from the pot into the main cage, investigated, chewed and manipulated the sheet. Although not recorded systematically, this gave a strong impression that the paper was immediately more attractive than the fibre.

The cages were scanned a total of 1305 times when the nesting materials were present. The mice were recorded as active during 24.7% of these. Table 2 shows that the most frequently constructed nest was built under the feeder and comprised a mixture of both the fibre and paper. Sawdust was usually present in the nests, though this appeared to be due to the trapping nature of the fibrous material rather than having been deliberately incorporated by the mice. The second most frequently built nest, also a mixture of the materials, was situated in the main area of the cage i.e. with no overhead cover other than that provided by the nest.

All 39 mice used one or both of the materials to construct a nest. Two mice constructed their nest entirely of paper while all the remainder constructed their nest from a mixture of the paper and the fibre. The nests were built rapidly; 36 mice built a nest during the first dark phase after the materials were initially placed in the cages and 37 mice built nests during the first dark phase after fresh materials were provided. The longest period that elapsed before a nest was built was 72 h.

There was a strong tendency to construct the first nest in the same location as the site chosen for sleeping prior to the materials being placed in the cages; 25 nests were built in the same location, 4 changed to a location in one of the pots, 4 changed to a different location for no obvious reason, and 6 mice had previously slept at the rear of the cage

thus necessitating a change in location because the pots occupied this position.

The mice were also conservative in their choice of nest location after fresh nesting materials were supplied. Twenty-one built their second nest in the same location after the first nest was removed. Of the 18 mice which were recorded as changing site, this included 10 which changed to building their nests in one of the pots. In addition, it should be noted that a change in site between 'feeder' and 'drinker' (and to a lesser extent 'other' areas of the cage) might in reality have required a change in location of only a few centimetres.

The nests built by the mice varied in size and complexity. Two individuals constructed simple mats and slept on top of these whereas all the other nests provided overhead shelter with varying densities of cover. Some nests were constructed with an entrance/exit tunnel and an enclosed, central sleeping chamber: others were a simple aggregation which the mouse sheltered under. Most of the nests appeared to be a homogenous accumulation of the fibrous material and shredded pieces of the paper, though 3–4 nests were more highly organized in that the paper was apparently used to line the inside of the nest while the fibre formed the major external structure. The mice generally used all the materials available, however, three of the mice left some of the fibrous material unused in the pot for several days.

Discussion

The principal finding of this study is that when 39 non-breeding mice were provided with nesting materials, each individual rapidly and spontaneously performed complex nest-building behaviours and constructed a nest. This was despite the mice having no prior experience of these materials or the opportunity to build nests other than heaping sawdust provided as floor substrate (see Sherwin 1996a). This indicates that housing non-breeding mice without nesting materials precludes them from performing a behaviour which is either innate or quickly learnt by a great proportion of laboratory mice (strain and sex differences notwithstanding).

The present study was conducted using individually housed female mice, a form of housing rarely practised in laboratories. Extrapolation of these findings to group housed animals therefore needs to be examined, though previous reports (Koller 1956, Lynch & Possidente 1978) and unpublished observations during pilot trials for this study indicate that group housed females also spontaneously build non-maternal nests.

The findings of this study support other work which indicates the welfare of laboratory mice may be improved if we provide them with nest-building material. Firstly, it has been argued (e.g. Dawkins 1990, Sherwin & Nicol 1996) that animals are more likely to experience suffering if we do not provide them with resources for which they are highly motivated. It has been shown that mice will repeatedly build nests which are removed daily (Lee & Wong 1970, Lee 1973, Roper 1975a, Lynch 1977, Batchelder *et al.* 1982), they will work by lever-pressing to gain access to nesting material (Roper 1973, 1975abc, see also Jansen *et al.* 1969, Oley & Slotnick 1970) and will traverse aversive obstacles to gain access to deep sawdust (Sherwin & Nicol 1995, Sherwin 1996b). These observations indicate that mice are highly motivated to gain access to nesting material and/or perform nest-building behaviour. Although the motivation for gathering nesting material appears to be less strong than that for food, mice nonetheless will compensate for an increased work requirement to maintain their nest-building behaviour (Roper 1975b). Secondly, the function of non-maternal nests may be directly related to welfare which is negated in the absence of suitable nesting materials. It is widely assumed that nest-building is thermoregulatory and this is supported by evidence that nest-building is more prevalent or more efficient at lower air temperatures (Lee & Wong 1970, Lynch 1973, Glaser & Lustick 1975, Lynch *et al.* 1976, Lynch & Possidente 1978, Batchelder *et al.* 1982, Rajendram *et al.* 1987), or is related to other thermoregulatory characteristics (Stephenson & Malik 1984, Lynch *et al.* 1986). But, it is illuminating to note an overwhelming number of studies have reported that non-maternal nest-build-

ing occurs at 21–26°C i.e. standard laboratory temperature or higher (Lee & Wong 1970, Van Oortmerssen 1971, Lynch 1973, 1977, Roper 1973, 1975abc, Voci & Carlson 1973, Estep *et al.* 1975, Glaser & Lustick 1975, Mulder 1975, Lynch & Possidente 1978, Lynch 1980, Batchelder *et al.* 1982, Lavery & Hay 1984, Stephenson & Malik 1984, Lynch *et al.* 1986, Rajendram *et al.* 1987, Blom 1993, van de Weerd 1994). The occurrence of nest-building at such air temperatures is perhaps not surprising considering the thermoneutral temperature of mice is 27–36°C (Glaser & Lustick 1975, Lynch *et al.* 1976, Stephenson & Malik 1984), but, this suggests that if we place mice in standard laboratory conditions of 21°C without providing nesting material, this precludes them from manipulating their micro-environment to preferred conditions. Thirdly, allowing mice to build nests might have non-thermal consequences which benefit welfare. For example, building a nest might allow the animal to remove itself from direct light and thus facilitate a reduction in retinal degeneration (Clough 1982), regulate auditory stimulation (Blom 1993), facilitate antipredator behaviour or camouflage (Rajendram *et al.* 1987), increase behavioural diversity or reduce extraneous stimulation.

These findings also support previous evidence that providing a pre-formed nest-box as a form of environmental enrichment may be inappropriate. Although some mice build nests in the pots and the impression was gained that these mice were less easy to disturb, the number of animals using the pots was relatively small. Previous reports have shown that mice are not highly motivated to use empty pots for sleeping in (Sherwin 1996b, Sherwin & Nicol 1996) and do not use tubular shelters unless loose floor substrate (sawdust) is removed (Sherwin 1996a). In conjunction with the present results and those of Roper (1975abc), it seems that manipulable material is preferred to a rigid, pre-formed shelter/nesting area.

The mice showed no clear preference for constructing nests of either the paper or the cellulosic fibrous material. However, selective use of the paper for lining some nests and the rapidity which this material was initially manipulated by the mice suggests the paper

might have had more attractive qualities. Mice can be highly discriminating in their choice of materials for nests. Roper (1975c) reported that mice differed in the amount of work they would perform for different widths of paper strip, and Blom (1993) reported that the preference of mice for shredded filter paper as bedding material was so great that it masked preferences between wood-chips. Mulder (1975) reported that pregnant female mice preferred bedding materials which were wood in origin. But, it appears that in general, if mice are offered a variety of materials for nest-building they will use a mixture (Van Oortmerssen 1971, Mulder 1975, present results). This might be due to investigators providing insufficient quantity of a single material, or possibly an attempt by the mice to camouflage the nest. Whichever, the probability remains that mice prefer to construct nests from a variety of materials.

The mice showed considerable individual differences in the shape and complexity of the nests they built, although individuals appeared to be consistent. Differences in the shape of non-maternal nests and the amount of material used have been described elsewhere (Voci & Carlson 1973, Lisk *et al.* 1969, Lavery & Hay 1984, Nee 1992) and it has been reported that significant strain and/or sex differences occur in the form of the nest or the amount of material used (Lee & Wong 1970, Lee 1973, Estep *et al.* 1975, Lynch 1977, Batchelder *et al.* 1982). The functional significance of these differences and their consequences on welfare have not been determined, although the shape and complexity of nests may be related to ambient temperature (Lee & Wong 1970, Glaser & Lustick 1975, Rajendram *et al.* 1987).

If nesting material is to be provided as a routine form of environmental enrichment, expense and practicality would be constraints. Based on retail prices, each paper nest cost approximately £0.005 and each fibre nest approximately £0.18. Since the mice had no clear preference for either of the materials, it seems appropriate to suggest that paper towels are a low-cost option for providing nesting-materials which may satisfy the predilection of mice for nest-building, though the possibility that a selection of materials

may be preferred deserves further attention and the composition and properties of the paper may need to be determined for some experimental protocols (e.g. see Potgieter & Wilke 1996). In the present study the paper towels were supplied by placing them in pots but it has been reported that if nesting material is placed in the feed hopper or on the roof of the cage, mice will tug this through the bars and subsequently use it for nest-building (Lee & Wong 1970, Lee 1973, Lynch 1973, 1977, 1980, Estep *et al.* 1975, Lynch & Possidente 1978, Lynch *et al.* 1976, Nee *et al.* 1992); this is clearly a more practicable method of providing nesting materials.

The present study examined the behaviour of only one strain of mice. Previous reports indicate that a wide variety of strains construct non-maternal nests when given the opportunity, namely, CPBs, c57Black/LiA, DBA/LiA, CBA/BrA (Van Oortmerssen 1971), C57Bl/6j, Swiss-Webster (Schneider *et al.* 1973, Rajendram *et al.* 1987), DBA/2j (Lee & Wong 1970, Schneider *et al.* 1973), RAP (Roper 1973, 1975abc), ARS Ha (ICR) Swiss mice (Mulder 1975), A/J, BALB/cJ, CBA/J, C3H/HeJ, C57BL/6J (Lee & Wong 1970, Estep *et al.* 1975, Lynch 1977, Batchelder *et al.* 1982), DBA/1J (Lynch 1977) C57BL/6Jlco, HS/lbg (Lynch & Possidente 1978, Lynch 1980, Batchelder *et al.* 1982), BALB/clbg, C3H2lbg (Batchelder *et al.* 1982), BALB/cBjlc (Blom 1993), C57BL/6JlcoU and BALB/cAnCryCpbRivU (van de Weerd 1994). I have found only three reports of mice not building nests; Lavery & Hay (1984) reported that on 3 of 220 scans, a nest was not built by C3H/HeGIF/Wehi or C3H/He inbred strains; Glaser & Lustick (1975) reported that nests were not built at ambient temperatures greater than 25°C; and Estep *et al.* (1975) reported that wild mice were significantly more likely not to build a nest than inbred strains. In conjunction with the present report, this indicates that when given the opportunity, nest-building is performed by a great proportion of non-breeding laboratory mice. Given the ease and inexpense of providing suitable nesting materials, the lack of evidence for detrimental effects and the prevalence and strength of

motivation to perform nest-building, it would seem that routinely providing paper towels as nesting material is an effective and inexpensive form of appropriate environmental enrichment for laboratory mice.

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References

- Batchelder P, Lynch CB, Schneider JE (1982) The effects of age and experiences on strain differences for nesting behaviour in *Mus musculus*. *Behavior Genetics* **12**, 149–59
- Blom HJM, Baumans V, Van Vorstenbosch CJAHV, Van Zutphen LFM, Beynen AC (1993) Preference tests with rodents to assess housing conditions. *Animal Welfare* **2**, 81–7
- Blom HJM (1993) *Evaluation of housing conditions for laboratory mice and rats*. PhD thesis, University of Utrecht, The Netherlands
- Bradshaw AL, Poling A (1991) Choice by rats for enriched versus standard home cages: plastic pipes, wood platforms, wood chips, and paper towels as enrichment items. *Journal of the Experimental Analysis of Behaviour* **55**, 245–50
- Brain PF (1992) Understanding the behaviours of feral species may facilitate design of optimal living conditions for common laboratory rodents. *Animal Technology* **43**, 99–105
- Broida J, Svare B (1983) Mice: progesterone and the regulation of strain differences in pregnancy-induced nest building. *Behavioral Neuroscience* **97**, 994–1004
- Castle JP, Marshall PE (1990) The captive management of a breeding colony of Ryuku mice (*Mus caroli*). *Animal Technology* **41**, 191–6
- Clough G (1982) Environmental effects of research on animals used in biomedical research. *Biology Reviews* **57**, 487–523
- Dawkins MS (1989) Time budgets in Red Junglefowl as a baseline for the assessment of welfare in domestic fowl. *Applied Animal Behaviour Science* **24**, 77–80
- Dawkins MS (1990) From an animal's point of view: motivation, fitness, and welfare. *Behavioural and Brain Sciences* **13**, 1–61
- Estep DQ, Lanier DL, Dewsbury DA (1975) Copulatory behaviour and nest-building behaviour of wild house mice (*Mus musculus*). *Animal Learning & Behaviour* **3**, 329–36
- Farm Animal Welfare Council (1993) *Second report on priorities for research and development in farm animal welfare*. Tolworth: MAFF
- Glaser H, Lustick S (1975) Energetics and nesting behaviour of the northern white-footed mouse, *Peromyscus leucopus noveboracensis*. *Physiological Zoology* **48**, 105–13
- Jansen PE, Goodman ED, Jowaisas D, Bunnell BN (1969) Paper as a positive reinforcer for acquisition of a barpress response by the golden hamster. *Psychonomic Science* **16**, 113–14
- Koller G (1956) Hormonale und psychische Steuerung beim Nestbau weisser Mause. *Zool. Anzeig. Suppl.* **19**, 123–32
- Lacy RC, Lynch CB, Lynch GR (1978) Developmental and adult acclimation effects of ambient temperature on temperature regulation of mice selected for high and low levels of nest-building. *Journal of Comparative Physiology* **123**, 185–92
- Lavery KJ, Hay DA (1984) Electrophoretic, skeletal and behavioural divergence of two C3H substrains of mice. *Journal of Heredity* **75**, 171–4
- Lee CT (1973) Genetic analyses of nest-building behavior in laboratory mice (*Mus musculus*). *Behavior Genetics* **3**, 247–56
- Lee CT, Wong PTP (1970) Temperature effect and strain differences in the nest-building behaviour of inbred mice. *Psychonomic Science* **20**, 9–10
- Lisk RD, Pretlow RA, Friedmand SJ (1969) Hormonal stimulation necessary for elicitation of maternal nest building in the mouse (*Mus musculus*). *Animal Behaviour* **17**, 730–7
- Lisk RD (1971) Oestrogen and progesterone synergism and elicitation of maternal nest-building in the mouse (*Mus musculus*). *Animal Behaviour* **19**, 606–10
- Lynch CB (1973) Environmental modification of nest-building in the white-footed mouse, *Peromyscus leucopus*. *Animal Behaviour* **22**, 405–9
- Lynch CB (1977) Inbreeding effects upon animals derived from a wild population of *Mus musculus*. *Evolution* **31**, 526–35
- Lynch CB (1980) Response to divergent selection for nesting behaviour in *Mus musculus*. *Genetics* **96**, 757–65
- Lynch CB, Possidente BP, Jr (1978) Relationships of maternal nesting to thermoregulatory nesting in house mice (*Mus Musculus*) at warm and cold temperatures. *Animal Behaviour* **26**, 1136–43
- Lynch CB, Roberts RC (1984) Aspects of temperature regulation in mice selected for large and small size. *Genetical Research* **43**, 299–306
- Lynch GR, Lynch CB, Dube M, Allen C (1976) Early cold exposure: effects on behavioral and physiological thermoregulation in the house mouse *Mus musculus*. *Physiological Zoology* **49**, 191–9
- Lynch CB, Roberts RC, Hill WG (1986) Heterosis among lines of mice selected for body weight. 3. Thermoregulation. *Genetical Research* **48**, 95–100
- Mulder JB (1975) Bedding preferences of pregnant laboratory reared mice. *Behaviour Research and Instrumentation* **7**, 21–2

- Nee M, Rajendram EA, Brain PF (1992) Effects of sex and reproductive condition on nest building in four species of rodents. *The CEPNESP Bulletin* 1, 2-8
- Noirot E (1974) Nest-building by the virgin female mouse exposed to ultrasound from inaccessible pups. *Animal Behaviour* 22, 410-20
- Oley NN, Slotnick BM (1970) Nesting material as a reinforcement for operant behavior in the rat. *Psychonomic Science* 21, 41-3
- Porter WP, Busch RL (1978) Fractional factorial analysis of growth and weaning success in *Peromyscus maniculatus*. *Science* 202, 907-10
- Potgieter FJ, Wilke PI (1996) The dust content, dust generation, ammonia production, and absorption properties of three different rodent bedding types. *Laboratory Animals* 30, 79-97
- Rajendram EA, Brain PF, Parmigiani S, Mainardi M (1987) Effects of ambient temperature on nest construction in four species of laboratory rodents. *Boll. Zool.* 54, 75-81
- Roper TJ (1973) Nesting material as a reinforcer for female mice. *Animal Behaviour* 21, 733-40
- Roper TJ (1975a) Diurnal rhythms in the nest-building behaviour of female mice. *Behaviour* 52, 95-103
- Roper TJ (1975b) Nest material and food as reinforcers for fixed-ratio responding in mice. *Learning and Motivation* 6, 327-43
- Roper TJ (1975c) Self-sustaining activities and reinforcement in the nest building behaviour of mice. *Behaviour* 59, 40-57
- Scharmann W (1991) Improved housing of mice, rats and guineapigs: a contribution to the refinement of animal experiments. *Alternatives to Laboratory Animals* 19, 108-14
- Schneider JE, Lynch CB (1984) Investigation of a common physiological mechanism underlying progesterone-induced and maternal nesting in mice *Mus musculus*. *Journal of Comparative Psychology* 98, 165-76
- Schneider CW, Evans SK, Chenoweth MB, Beman FL (1973) Ethanol preference and behavioral tolerance in mice: biochemical and neurophysiological mechanisms. *Journal of Comparative and Physiological Psychology* 82, 466-74
- Sherwin CM, Nicol CJ (1995) Changes in meal patterning by mice measure the cost imposed by natural obstacles. *Applied Animal Behaviour Science* 43, 291-300
- Sherwin CM (1996a) Preferences of individually housed TO strain laboratory mice for loose substrate or tubes for sleeping. *Laboratory Animals* 30, 245-51
- Sherwin CM (1996b) Laboratory mice persist in gaining access to resources: a method of assessing the importance of environmental features. *Applied Animal Behaviour Science* 48, 203-14
- Sherwin CM, Nicol CJ (1996) Reorganisation of behaviour in laboratory mice (*Mus musculus*) with varying cost of access to resources. *Animal Behaviour* 51, 1087-93
- Stephenson SK, Malik RC (1984) Energy partitioning and growth in mice selected for high and low body weight. *Genetical Research* 43, 323-37
- van de Weerd HA, Baumans V, Koolhaas JM, van Zutphen LFM (1994) Strain specific behavioural response to environmental enrichment in the mouse. *Journal of Experimental Animal Science* 36, 117-27
- Van Oortmerssen GA (1971) Biological significance, genetics and evolutionary origin of variability in behaviour within and between inbred strains of mice (*Mus musculus*). *Behaviour* 38, 1-92
- Veasey JS, Waran NK, Young RJ (1996) On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. *Animal Welfare* 5, 13-24
- Voci VE, Carlson NR (1973) Enhancement of maternal behaviour and nest building following systemic and diencephalic administration of prolactin and progesterone in the mouse. *Journal of Comparative and Physiological Psychology* 83, 388-93
- Wainwright PE (1981) Maternal performance of inbred and hybrid laboratory mice (*Mus musculus*). *Journal of Comparative and Physiological Psychology* 95, 694-707