

## ORIGINAL PAPER

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**Male short-tailed field voles (*Microtus agrestis*) build better insulated nests than females**

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**Abstract** Nest construction is an extremely widespread behaviour. In small endotherms the nest serves primarily to provide insulation, and thereby retard heat loss of the constructor, or its offspring. In arctic and temperate regions many small mammals build nests to protect themselves from low ambient temperatures. We measured the physical properties of nests built by short-tailed field voles *Microtus agrestis* that were kept in captivity under cold conditions. The most important factor influencing nest insulation was nest wall thickness; however, nests with thick walls also contained more nesting material. Insulative capacity of the nest did not reach an asymptote up to nests containing 20 g of material. Nest insulation was not correlated with resting metabolic rate, body mass or body composition of the vole that constructed the nest. However, nests built by males had greater insulation than those made by females; males also had significantly lower food intake rates when compared to females with nests. No significant difference was observed in either fat mass or whole animal thermal conductance between males and females. Thermal conductance did increase significantly with increasing body mass, although not with resting metabolic rate. Voles with nests for prolonged periods had lower food intakes than voles without nests. The absolute saving averaged 1.9 g and was independent of body mass. This was a 28% saving on intake for a 22-g vole but only an 18% saving for a 40-g individual. When voles had nests for short periods they used the energy they saved to reduce food intake and increase body mass.

**Key words** Body mass · Body composition · Resting metabolic rate · Thermal conductance · Endotherms

**Abbreviations**  $C$  thermal conductance ·  $C_c$  cooling rate of control bottle ·  $C_e$  cooling rate of experimental bottle ·  $RMR$  resting metabolic rate ·  $RMR_{tmz}$  resting metabolic rate in thermoneutral zone (25 °C)

**Introduction**

Modification of the environment by animals through the construction of nests, that provide protection from predators (e.g. Kern et al. 1993) or shelter from environmental extremes, is a widespread behaviour found in representatives from most vertebrate groups (e.g. fish, amphibia, reptiles, birds and mammals) and many invertebrate groups (e.g. insects and spiders). Among the most intricate nesting structures are the nests built by small endotherms. Because of their small size, these animals have high surface to volume ratios and, when this is combined with their high body temperatures, this leads to relatively high heat loss compared to larger animals (Davenport 1992).

The primary function of nests constructed by small endotherms appears to be to reduce heat loss of themselves, or of their offspring, by increasing the external insulation available whenever the animals are resting (Hayward 1965; Layne 1969; Gebczynska and Gebczynski 1971; Casey 1981; Vogt and Lynch 1982; Rychlik and Korda 1989; Lombardo et al. 1995; but see Ellison 1995). Direct measurements confirm that nests generally provide considerable thermal benefits, thereby reducing energy expenditure (Stebbins 1977; Vogt and Lynch 1982; Stapp et al. 1991; Kern et al. 1993) and increasing survival (Sealander 1952). Buttemer et al. (1987) reported that metabolic rates of Verdins *Auriparus flaviceps* were 52% higher, at 5 °C, outside the nest than inside. However, they calculated that only around 10% of this reduction in metabolic rate was due to the retention of metabolically warmed air in the nest

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and that the insulative properties of the nest itself were more important in reducing heat loss in these small birds at low temperatures.

During winter, in the temperate and arctic regions, many small endotherms become more social in their behaviour, and may roost communally or huddle with conspecifics (Baudinette 1972; Morton 1978; Karasov 1983; Stapp et al. 1991; Berteaux et al. 1996). This strategy leads to a reduction in the exposed surface area of the animals (Vickery and Millar 1984; Canals et al. 1989) and to localised heating of the microhabitat (Walsberg 1985, 1990), both of which contribute to a reduction in energy demands (Contreras 1984; Bazin and MacArthur 1992; Hayes et al. 1992). The effect of huddling on the local microclimate is enhanced if the huddled animals also occupy a nest, which can trap their body heat (Sealander 1952; Stapp et al. 1991). The benefits of winter nesting, however, may be most important for solitary animals (Chappell 1980; Casey 1981; Buttemer et al. 1987) which cannot derive benefits from huddling. Nest construction is probably also important during the summer in many arctic and temperate zone small mammals, since at least some have been shown to maintain their thermogenic capacity all year round (Haim et al. 1995), presumably because ambient temperatures remain substantially below their lower critical temperature even in mid-summer.

Larger nests provide better insulation (Grubbauer and Hoi 1996), and selection may therefore favour animals that construct large nests (Bult and Lynch 1997). However, it has been suggested that the thermal benefits of adding more material becoming progressively lower as the nest gets larger. Nest size may therefore reflect a trade-off between the reduced expenditure attained when living within the nest, compared with the increased energy consumption due to prolonged exposure to adverse conditions whilst collecting material to build it (Glaser and Lustick 1975). Costs of construction are likely to increase linearly with the amount of nest material added to the nest, but benefits may reach an asymptote.

This balance in costs and benefits might be expected to vary with the individual attributes of the nest builder. Exactly what effects individual attributes might have, however, is a matter of interpretation. For example, larger individuals on average have higher absolute metabolic rates at low temperatures than smaller individuals (reviewed in Speakman 1995) and thus might be predicted to derive more benefit from reducing their expenditures to basal (thermoneutral) levels. This analysis would predict that larger individuals should build larger nests. On the other hand it has been suggested that because smaller individuals have higher mass specific energy expenditures they would benefit more from constructing larger nests (McCracken et al. 1997).

The primary aim of this experiment was to measure the physical properties (mass, wall thickness and shredding of bedding material) of nests built by short-tailed field voles *Microtus agrestis* and to relate these to direct measurements of nest insulation. The second aim

was to assess the extent to which individual attributes of the voles constructing the nests [body mass, resting metabolic rate (RMR) and body composition] affected nest insulative properties. The final aim was to quantify the energetic benefits that accrue to voles that are provided with materials to construct nests, in terms of their body mass and food intake.

## Materials and methods

A population of short-tailed field voles *M. agrestis* was captured in north-east Scotland (57°N), during September and October (1997). The animals were brought into captivity, and individually housed in cages containing sawdust and woodwool bedding. The voles were provided, ad libitum, with water and a pelleted rodent diet (rat and mouse number 1 maintenance diet, Special Diets Services, BP Nutrition, UK), and were kept in the cold (mean temperature  $8 \pm 4$  °C). Voles were allowed at least 3 weeks to adjust to captive conditions before any experimental procedures were carried out.

### Effects of individual attributes on nest building

This experiment commenced in November (1997). At the start of the experiment, all bedding was removed from the cages of 30 animals (17 males and 13 females), and fresh woodwool bedding (ca. 20 g) was placed inside the food hopper for a period of 48 h. This provided the animals with access to surplus bedding material thereby allowing them to remove as much as they wanted to construct new nests. After 48 h, nests that had been built were removed, weighed and tested for their insulating properties (as described below). Body mass, body composition, food intake and RMR (measured within the thermoneutral zone,  $RMR_{tnz}$ ) of each individual were measured during the week prior to the construction of nests.  $RMR_{tnz}$  was measured during the light phase over a period of 2 h, using an open circuit respirometry system (Servomex). Voles were not denied access to food and water before respirometry was performed. Air was drawn through the apparatus at a rate of 600–800 ml/min and dried using silica gel before passing through the animal chamber which was within an incubator (Gallenkamp) set at  $30 \pm 0.5$  °C (thermoneutral for these animals). Excurrent air was dried and a sub-sample of 150 ml passed through the oxygen analyser. Carbon dioxide was not absorbed (Koteja 1996a), to maximise accuracy in the derived estimate of energy expenditure. Mean measurements from the oxygen analyser were recorded on a microcomputer at 30-s intervals. The ten lowest consecutive readings (equivalent to 5 min within the respirometry chamber) were then used to estimate  $RMR_{tnz}$  for each measurement, employing the appropriate equation from Hill (1972) and corrected for temperature and pressure. The mean of three measurements from consecutive days was used as an evaluation of  $RMR_{tnz}$  for each vole. Day-to-day repeatability was calculated over the three measurements and the coefficient of variation averaged 13%. Body composition was measured by total body electrical conductivity (TOBEC) (Koteja 1996b) using an ACAN-2 small animal body composition analyser (Jagmar). Lean mass was calculated using an equation derived from a calibration experiment (P.I. Mitchell, C. Hambly and J.R. Speakman, unpublished data) in which 20 voles were measured using the ACAN-2 and then killed. Fat-free mass was determined for these voles by using the Soxhlet method of fat extraction and regressed against the reading obtained using TOBEC. Lean mass therefore included skeletal material and fat mass was extracted fat.

### Determination of thermal conductance ( $W/^\circ C$ )

A sample of 20 mature adult voles (males,  $n = 10$ ; females,  $n = 10$ ), acclimated to a constant cold temperature ( $8 \pm 3$  °C)

were used during this experiment. To calculate thermal conductance ( $C$ ), RMR was determined at four different incubator (Gallenkamp) temperatures (25 °C, 20 °C, 10 °C and 0 °C) using open-flow respirometry (see section above). RMR was measured for 1h at each of the four temperatures, with a minimum period of 30 min between each temperature change to enable the voles to adjust to the new temperature. RMR data collected during these periods of adjustment were not included in the subsequent analyses, and the total time an individual resided in the metabolic chamber never exceeded 6 h. The chamber temperature at which an RMR run commenced alternated daily, starting at either 25 °C or 0 °C. Data was corrected for standard temperature and pressure and then RMR at each temperature was calculated using the lowest ten 30-s readings recorded at that particular temperature. Prior to a measurement of RMR, all voles were weighed (Sartorius, 0.01 g) and body temperature was recorded using a rectal probe (Digitron, 2751-K).

#### Effect of nest building on food intake and body mass under cold conditions – long term provision of nesting material

Data was collected over two seasons. A sample of ten voles, captured in November (1996), were bought into captivity and housed in a constant temperature room maintained at  $8 \pm 3$  °C with a photoperiod of 16L:8D. Food, water and bedding material were provided ad libitum. The voles were allowed to acclimate to the new conditions for a period of 10 weeks, with bedding material always available. Food intake and body mass were measured for each vole at the beginning and the end of the acclimation period. Food intake was calculated as the amount of food that went missing from the food hopper over a period of 1 week. Cages and nests were checked for food and food found within them was weighed and accounted for. A second group of voles ( $n = 18$ ) captured in October (1997) were treated in exactly the same manner except no bedding material was provided. All measurements of food intake and body mass were made using a portable balance accurate to 0.1 g (Sartorius).

#### Effect of nest building on food intake and body mass under cold conditions – short-term provision of nesting material

This experiment involved a sample of 16 male voles acclimated to cold temperature ( $8 \pm 4$  °C) and housed under a long photoperiod (16L:8D). All males were mature adults in reproductive condition, as judged by the presence of visible testes, and had been kept under these conditions for a period of 6 months. Each male was initially housed in a cage (dimensions =  $45 \times 15 \times 12$  cm) containing sawdust but no bedding material, and was provided with pelleted food and water ad libitum. The food remaining in the hopper of each cage was measured twice (between 2 p.m. and 3 p.m.) during the 1st week, and food intake was calculated as the difference in food remaining after each measurement. The cages were checked for hoarded food at the time of each measurement; any food found within the cage was removed and weighed, with appropriate adjustments being made to the calculation of food intake. After 1 week, the voles were allowed access to nesting material for 2 days by placing ca. 20 g of woodwool bedding on the lid of each cage. Nests constructed during the 2-day period were left in the cage and unused bedding was removed. Food remaining in the hopper was then measured twice during the 2nd week, with food intake per day calculated as before. Body mass of the voles was measured twice within the 1st week, and three times at the end of the 2nd week. All measurements were made using a portable balance accurate to 0.01 g (Sartorius).

#### Assessment of nest insulation

Nest insulation was measured in an incubator (Gallenkamp) set at  $9 \pm 1$  °C. Glass bottles (diameter 2.2 cm, length 4.6 cm, volume  $17.5 \text{ cm}^3$ , surface area  $39.4 \text{ cm}^2$ ) were used as substitute 'voles'.

Each bottle was fitted with a plastic lid through which a temperature probe with an accuracy of 0.1 °C (Digitron Instrumentation) was inserted. Two bottles were filled with water heated to a temperature of  $42 \pm 2$  °C; one was inserted into the nest and the second placed inside the incubator without a nest. A third probe was used to measure air temperature inside the incubator.

The time was recorded at each degree interval as the bottles cooled from 37 °C to 20 °C. Air temperature inside the incubator, which was stable throughout the measurements, was measured every 2 min and the mean calculated. The elevation of the temperature of the water within the bottles above ambient was calculated by subtraction of mean air temperature and the exponential approach to ambient temperature linearized by log transformation (Bakken 1976). The time constant of this 'cooling curve' was used as a measure of the rate at which the water in each bottle cooled down. An assessment of the insulative capacity of the nest was calculated from the ratio of the cooling rates of the control and experimental bottles using the following equation:

$$\text{Insulation index} = C_c/C_e \quad (1)$$

where  $C_c$  was the cooling rate of the control bottle (with no nest) and  $C_e$  was the cooling rate of the experimental bottle within the nest. Nest mass and wall thickness were measured for each nest, and the nest was scored (1 or 0) according to whether the vole had shredded its bedding material into thinner, shorter strips. Body mass, RMR and sex of the voles were also recorded.

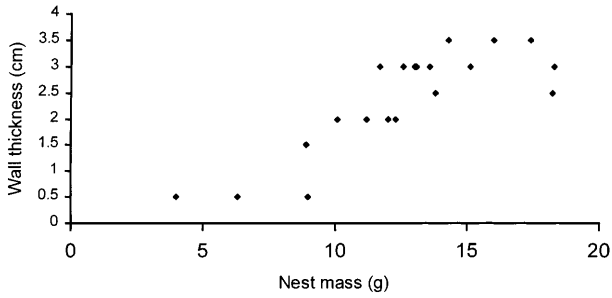
## Results

### Nest building under experimental conditions

When provided with ca. 20 g of bedding all 30 voles built round ball-like nests. In most cases (26/30), some or all of the woodwool was shredded. Completely shredded nests did not retain their structure and fell apart when they were removed from the cage. Of the 30 nests, one (from a male) was flooded and therefore unusable, and a further nine nests were made from completely shredded material. These latter nests did not retain their structure and were excluded from measurements of insulation properties, although five were used for measurements of nest mass. In total, insulation was measured for 9 nests made by males and 11 nests made by females.

### Nest attributes affecting nest insulation

Measurements of nest wall thickness and nest mass were both negatively skewed, so the data were squared to normalise the distributions. Wall thickness<sup>2</sup> and nest mass were strongly correlated (Fig. 1). Thus voles appeared only able to increase the wall thickness of their nests by incorporating more material into the nest. Both these attributes were correlated with the nest insulation index (Fig. 2a, b). We entered these variables as independent predictors in a generalised linear model analysis along with the presence or absence of shredding of the nest material (scored 1 or 0). Only wall thickness<sup>2</sup> had a significant effect on nest insulation and explained 47% of the variation in nest insulation ( $F_{1,18} = 16.15$ ,  $P = 0.001$ : Fig. 2a). None of the interactions between the predictor variables were significant.



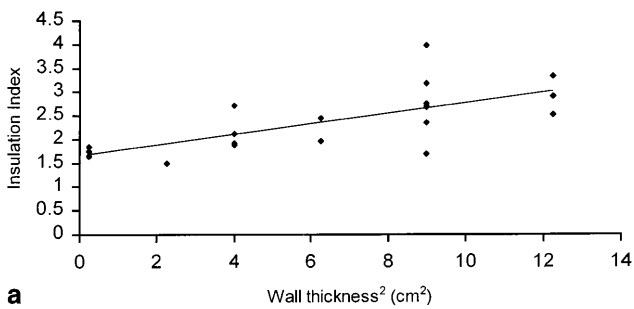
**Fig. 1** Relationship between wall thickness of nests built by short-tailed field voles and the mass of material (wood wool) incorporated into the nest

Individual attributes affecting nest insulation

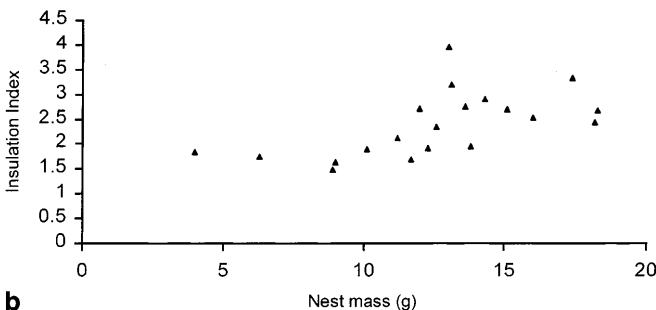
There was no significant effect of body mass ( $F_{1,11} = 0.53, P = 0.480$ ),  $RMR_{tnz}$  ( $F_{1,11} = 0.18, P = 0.676$ ), or percentage body fat (Arcsine transformed,  $F_{1,11} = 0.12, P = 0.734$ ) of the vole on the insulation of the nest it built (General Linear Model: GLM), with no significant interactions between any of the variables. However, nests made by males had a significantly greater insulation index than those made by females (ANOVA:  $F_{1,18} = 5.34, P = 0.033$ ). The mean insulation index for nests made by males was  $2.7 \pm 0.2$  SE, whereas the insulation index of nests made by females was  $2.1 \pm 0.2$  SE (Fig. 3).

Effects of individual attributes on C

Males and females did not differ significantly in either body mass ( $t_{18} = -0.015, P = 0.988$ ) or in rectal body

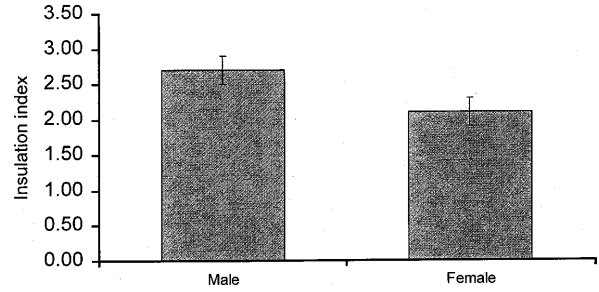


**a**



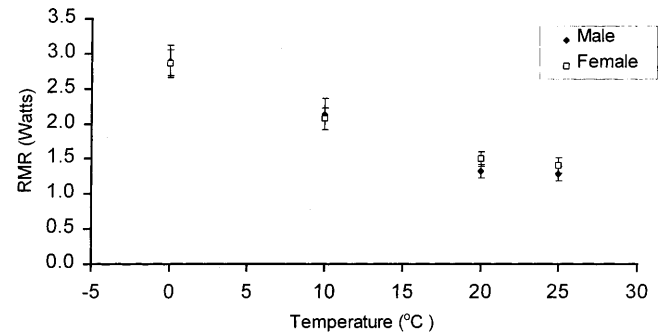
**b**

**Fig. 2** Insulation index of nests built by short-tailed field voles plotted against **a** wall thickness<sup>2</sup> and **b** nest mass. In univariate analyses both wall thickness and body mass were correlated with the insulation index of the nest. (In multivariate analyses only wall thickness was significant)

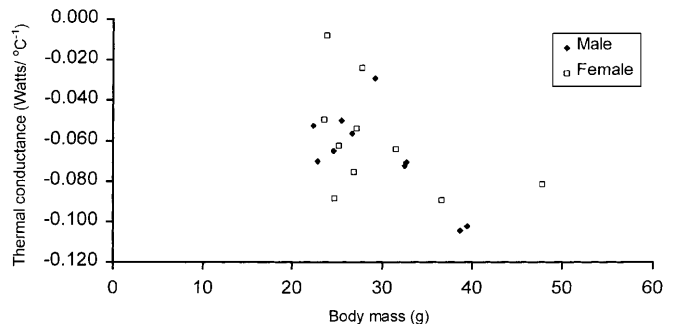


**Fig. 3** The mean insulation index of nests made by male voles in comparison to nests made by female voles. Nests made by males had a significantly greater insulation index ( $F_{1,18} = 5.34, P = 0.033$ )

temperature ( $t_{18} = 1.143, P = 0.271$ ) measured immediately prior to an RMR measurement. Figure 4 shows the mean ( $\pm$  SE) calculated RMR at 25 °C, 20 °C, 10 °C and 0 °C, and mean ( $\pm$  SE) C of male and female voles. Sex had no significant effect on C (ANCOVA:  $F_{2,19} = 0.67, P = 0.425$ ), however, there was a significant correlation (Fig. 5) between C (W/°C) and body mass ( $r_{20} = -0.562, P = 0.010$ ). C was higher (more negative) in heavier individuals. No relationship was found between C and RMR measured at 25 °C ( $r_{20} = 0.171, P = 0.471$ ). No significant interaction



**Fig. 4** Mean ( $\pm$  SE) resting metabolic rate measured at 25 °C, 20 °C, 10 °C and 0 °C in male and female *Microtus agrestis*. Mean ( $\pm$  SE) thermal conductance (slope) calculated was  $-0.067 (\pm 0.007)$  and  $-0.060 (\pm 0.009)$  for males and females respectively ( $n = 10$  in each case)



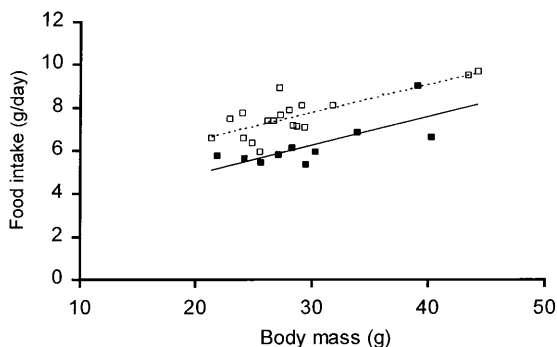
**Fig. 5** The significant relationship between thermal conductance (W/°C) and body mass (g) in male and female voles ( $n = 20$ )

between body mass and sex effects on  $C$  ( $F_{1,19} = 0.48$ ,  $P = 0.499$ ) was found.

#### Effect of long-term access to nests on food intake

Voies with nests did not have significantly lower (mean  $\pm$  SE) body masses ( $21.83 \pm 1.489$  g) than individuals without nests ( $24.70 \pm 1.405$  g;  $F_{1,28} = 2.38$ ,  $P = 0.135$ ). Food intake of cold-acclimated voies was significantly correlated with body mass (GLM,  $F_{1,24} = 26.02$ ,  $P < 0.001$ , Fig. 6), the presence of a nest ( $F_{1,24} = 29.45$ ,  $P < 0.001$ ) but not sex of the vole ( $F_{1,24} = 0.70$ ,  $P = 0.412$ ). There was no significant effect on food intake of the interaction between body mass and the presence or absence of the nest. The absolute benefits in reduced food intake of having a nest were therefore independent of body mass and averaged 1.9 g. Since, in the absence of nests, smaller voies had lower food intakes, the relative benefits of the nests were greater for small voies. On average, having a nest reduced the food intake of a 22-g vole by 28% but reduced the food intake of a 40-g vole by only 18%. No effect was seen between nest presence or absence and gender (GLM,  $F_{1,28} = 0.02$ ,  $P = 0.90$ ).

Male voies with nests ate significantly less food ( $F_{1,21} = 4.890$ ,  $P = 0.04$ ) than females with nests ( $5.96 \pm 0.336$  g/day and  $7.02 \pm 0.345$  g/day respectively), although no difference in mass gain was seen between males and females ( $F_{1,21} = 0.790$ ,  $P = 0.384$ ). No significant differences were seen between males and females (mean  $\pm$  SE) in either body mass (males  $20.556 \pm 0.621$  g, females  $20.933 \pm 0.333$  g;  $F_{1,21} = 0.790$ ,  $P = 0.384$ ), lean mass (males  $13.837 \pm 0.386$  g, females  $15.102 \pm 0.361$  g;  $F_{1,21} = 1.770$ ,  $P = 0.202$ ) or in fat mass (males  $6.719 \pm 0.856$  g, females  $5.831 \pm 0.305$  g;  $F_{1,21} = 0.280$ ,  $P = 0.603$ ).



**Fig. 6** Food intake as a function of body mass for voies with and without nests (open squares/dashed line = no nests, closed squares/complete line = with nests). No difference was seen between the regression line slopes (MANOVA,  $F_{1,28} = 0.01$ ,  $P = 0.942$ ) but a significant difference existed between the regression line elevations ( $F_{1,28} = 32.34$ ,  $P = 0.0001$ ). Voies with nests ate less food and the reduction was independent of body mass

**Table 1** Mean food intake (FI) and body mass (BM) of 16 male voies when housed for 1 week without nesting material and then 1 week with nesting material at 8 °C ( $\pm$ SD)

Male	Without nest		With nest	
	Mean FI (g/day)	Mean BM (g)	Mean FI (g/day)	Mean BM (g)
1	5.5 $\pm$ 0.3	29.3 $\pm$ 0.3	5.3 $\pm$ 0.6	30.2 $\pm$ 0.5
2	8.7 $\pm$ 0.4	33.3 $\pm$ 0.8	6.9 $\pm$ 0.3	34.2 $\pm$ 0.5
3	8.2 $\pm$ 0.9	38.8 $\pm$ 0.1	7.7 $\pm$ 0.6	40.8 $\pm$ 0.4
4	8.9 $\pm$ 0.5	36.0 $\pm$ 0.1	7.6 $\pm$ 0.5	36.1 $\pm$ 0.4
5	6.7 $\pm$ 0.5	28.8 $\pm$ 0.6	6.2 $\pm$ 0.4	30.1 $\pm$ 0.2
6	8.6 $\pm$ 0.4	29.3 $\pm$ 0.1	6.9 $\pm$ 0.5	29.4 $\pm$ 0.3
7	8.8 $\pm$ 0.1	26.2 $\pm$ 0.1	8.3 $\pm$ 0.1	27.5 $\pm$ 0.2
8	5.9 $\pm$ 0.1	21.2 $\pm$ 0.1	4.3 $\pm$ 0.2	20.4 $\pm$ 0.4
9	5.3 $\pm$ 0.4	24.2 $\pm$ 0.1	7.2 $\pm$ 0.7	25.4 $\pm$ 0.4
10	10.1 $\pm$ 0.5	23.0 $\pm$ 0.6	10.0 $\pm$ 0.1	24.6 $\pm$ 0.2
11	9.1 $\pm$ 0.1	32.9 $\pm$ 1.1	5.9 $\pm$ 0.5	33.4 $\pm$ 0.6
12	8.3 $\pm$ 0.2	24.4 $\pm$ 0.8	7.1 $\pm$ 0.1	26.8 $\pm$ 0.3
13	9.3 $\pm$ 0.2	23.6 $\pm$ 0.9	10.0 $\pm$ 0.9	22.9 $\pm$ 0.1
14	8.8 $\pm$ 0.1	23.6 $\pm$ 0.9	4.8 $\pm$ 3.3	24.2 $\pm$ 1.1
15	10.2 $\pm$ 0.1	31.1 $\pm$ 1.4	8.0 $\pm$ 0.4	32.5 $\pm$ 0.8
16	7.7 $\pm$ 0.2	24.2 $\pm$ 0.6	6.7 $\pm$ 0.1	25.2 $\pm$ 0.3

#### Short term changes in body mass and food intake after nest building

The food intake in male voies significantly decreased (paired  $t$ -test  $t_{16} = 2.792$ ,  $P = 0.007$ ) and body mass significantly increased (paired  $t$ -test  $t_{16} = 3.869$ ,  $P = 0.0008$ ) when nests were present within the cages (Table 1). There was no significant relationship ( $r_{16} = 0.127$ ,  $P > 0.05$ ) between the change in food intake and the change in body mass that occurred between periods when the nest was absent and present.

## Discussion

Of the properties tested, the most significant factor influencing nest insulation was wall thickness. Nest mass, however, was also correlated with insulation, since increases in wall thickness were only possible if more nesting material was used. This result would be expected from heat transfer theory, and has been assumed in many studies of nest function (e.g. Baxter 1996; McCracken et al. 1997) and found in other studies (e.g. Grubbauer and Hoi 1996). However, Ellison (1995) found no correlation between nest size and  $C$  of nests built by the pouched mouse *Saccostomus campestris*. In our study, insulative properties of the nests continued to increase with increases in wall thickness (and nest mass) up to nest masses of at least 20 g. This may also appear to conflict with observations that the energetic benefits of nests built by white footed mice *Peromyscus leucopus* did not increase for nests larger than about 13 g (Glaser and Lustick 1975). The difference between these latter results probably reflects the different methods of quantifying the properties of the nests. In our study we measured insulation directly, while in the study of

Glaser and Lustick (1975) 'benefit' was quantified as the energetic benefit derived by the animals inside the nests. Energy expenditure is a function of the temperature inside the nest (Stebbins 1977; Vogt and Lynch 1982). Therefore, once a nest reaches a certain insulative capacity where the internal temperature rises to thermoneutral, addition of further material to the nest will continue to enhance its insulative properties, but would not energetically benefit the animal, which reaches its lowest energy demands in the thermoneutral zone. Indeed very large nests may be disadvantageous because they may cause overheating.

It was unexpected that of the physical attributes measured (namely body mass,  $RMR_{tnz}$ , percentage body fat and sex) only sex had any influence on the insulation of the nests that were built, with males building better (more insulated) nests than females. Of the 30 original nests we could not use 9 because they were highly shredded, and did not retain their structure when removed from the cages. Of these nine shredded nests, seven were from males; therefore there may have been a bias in the selection of nests which caused the sex effect. This seems unlikely, however, because the extent of shredding in those nests we did measure did not affect the thermal conductivity of the resultant nests. Body mass might have been expected to influence the  $C$  of the nest because it was correlated with whole animal  $C$ . Moreover, in wood mice *Apodemus sylvaticus* there is a positive link between thermogenic capacity and  $RMR_{tnz}$  (Speakman 1995). This might also have been expected to precipitate a link between  $RMR_{tnz}$  and nest building, if the same relationship holds in field voles, because animals with lower  $RMR_{tnz}$  and lesser thermogenic capacity might need to build better nests. Neither of these effects were found in our study.  $C$  was independent of vole sex, suggesting the effect of sex on nest building was not caused by differences in their whole body  $C$ . The reasons why males built better insulated nests than females therefore remain obscure.

Long-term availability of nest material resulted in a decrease in food intake for voles with nests, compared to those without nests and a decrease in food intake in male voles with nests compared to females with nests. The absence of an effect of body mass on this decrease is consistent with the fact we observed no effect of vole body mass on the insulative properties of the nests they built. Although larger voles have greater food requirements than smaller voles, when they are deprived of nesting material, they appeared unable to derive greater benefits by constructing bigger nests with thicker walls. This was not because of a lack of nesting material, because the voles did not use up all the material they had been provided with. Perhaps the nests built by both small and large voles in this experiment were adequate to raise the internal nest temperature to thermoneutral. Therefore both large and small voles derived the maximum possible benefits.

Almost all the male voles provided with nest material for a period of 1 week (15/16), reduced their food intake

after the addition of nesting material. However, unlike in the longer-term experiment, these individuals also adopted a strategy of increasing their body mass after the addition of nest material, despite reducing their food intake. This experiment highlights that the energetic benefits that accrue from nesting behaviour, at least over the short-term, can be used in different ways and may lead to both a reduction in food intake and an increase in body mass.

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