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Working with what you've got: Changes in thermal preference and behavior in mice with or without nesting material

Brianna N. Gaskill [a,*], Stephanie A. Rohr [a], Edmond A. Pajor [a,1], Jeffrey R. Lucas [b], Joseph P. Garner [a]

[a] Animal Behavior and Well-Being Group, Department of Animal Science, Purdue University, 125 S. Russell St, West Lafayette, IN 47907, USA
[b] Department of Biological Sciences, Purdue University, 915 W. State Street, West Lafayette, IN 47907, USA

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ABSTRACT

In laboratories mice are typically housed at ambient temperatures (T_a) of 20–24 °C, which are below their average preferred T_a of ≈30 °C. Adjusting laboratory T_a is not a solution because preferences differ depending on activity, time of the day, and gender. We tested the hypothesis that providing mice with nesting material will allow behavioral thermoregulation and reduce aversion to colder T_a. We housed C57BL/6J mice with and without nesting material in a set of 3 connected cages, each maintained at a different T_a (20, 25, or 30 °C). Mice were confined in and given free access to the T_a options to determine if thermotaxis or nest building was the primary mode of behavioral thermoregulation. As predicted, nesting material reduced aversion to 20 °C but the overall preference, in both treatments, was still 30 °C. Inactive and nesting behaviors were more likely to be seen in contact with nesting material while active behaviors were more likely to be observed when not in contact. Nest quality increased with decreasing T_a when mice could not use thermotaxis but nest quality was uncorrelated with T_a when thermotaxis was possible. Males decreased nest quality with increasing temperatures but females showed no correlation. We conclude that nesting material does not alter thermal preferences for 30 °C when thermotaxis is possible, indicating thermotaxis as the primary mode of behavioral thermoregulation. However, when thermotaxis is not possible, mice adjust nest shape depending on the T_a. Nesting material appears to partially compensate for cooler T_a and is especially important when mice are inactive. Therefore, nesting material may be a solution to the mismatch between laboratory T_a and mouse thermal preferences.

1. Introduction

Mice under standard laboratory conditions are generally housed between 20 and 24 °C (Gordon, 1993, 2004), which is below their lower critical temperature of ≈30 °C (Gordon, 1993). When the ambient temperature falls below a mammal's lower critical temperature, the metabolic rate is increased so that heat production by the body matches heat loss to the environment to maintain a constant body core temperature (Gordon, 1993). The thermal preference of a single mouse, measured by the amount of time spent in a temperature, is also ≈30 °C but is not strongly altered when mice are group housed (≈29 °C, Gordon et al., 1998). Therefore, mice under standard laboratory conditions must burn additional energy to stay warm. This inescapable challenge to homeostasis is by definition stressful (Moberg, 2000) and can compromise many aspects of physiology. For instance, mouse immune function is impaired at 20 °C and pup growth is impaired at 18 °C (Yamauchi et al., 1983; Gordon, 1993). In addition, extreme cold stress has been shown to alter behavior, metabolic parameters (Yamauchi et al., 1983; Banet, 1988), body composition (Chevillard et al., 1963; Swiergiel, 1987), and increase body temperature variability (Yang and Gordon, 1996). These alterations to normal function will affect scientific outcomes.

Previous research using a thermal gradient shows that mice prefer warmer temperatures, near 30 °C (Gordon, 1993). The same preferences exist when mice are tested in laboratory cages (Gaskill et al., 2009). Furthermore, previous findings indicate that mouse home cage temperature preferences differ for different behaviors, time of the day, and between sexes (Gaskill et al., 2009). Therefore, simply adjusting laboratory temperatures is not the solution. In the wild, a mouse's first response to thermal stress is behavioral: they respond to both heat and cold with thermotaxis (locomotion away from stressful temperatures), to heat with fur licking, and to cold with huddling and nest building (Gordon, 1993; Latham and Mason, 2004). Providing laboratory mice with nesting material would serve as a way for mice to alleviate

* Corresponding author. Tel.: +1 765 494 4828; fax: +1 765 494 9347.
E-mail address: bgaskill@purdue.edu (B.N. Gaskill).
[1] Present Address: Department of Production Animal Health, Faculty of Veterinary Medicine, University of Calgary, 3280 Hospital Drive NW, Calgary Alberta, Canada T2N 4N1.

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thermal stress by allowing them to control their environment without altering ambient temperature. When mice are provided with suitable nesting material in typical laboratory conditions, they consume less food and weigh more, which is consistent with a reduction in energy being burned for thermogenesis (see Olsson and Dahlborn, 2002). Furthermore, mice alter nest shape due to ambient temperature, building dome-like nests in cooler temperatures and open or cup shaped nests as temperatures increase (Lynch and Hegmann, 1973; Wolfe and Barnett, 1977; Lynch and Roberts, 1984). Based on these results it is likely that nesting material allows for more efficient thermoregulation. However, it is unknown if access to nesting material will alter thermal preferences or whether mice will preferentially respond to temperature changes with nest building or with thermotaxis. Such alterations in thermal preference are found in humans wearing insulating clothing, where it can be decreased by nearly 15 °C (Faerevik et al., 2001).

The goal of this experiment was to test the hypothesis that nesting material would allow for behavioral thermoregulation and thus alter thermal preferences. We predicted that the amount of time spent in temperatures below the lower critical temperature (20 and 25 °C) would increase due to improved thermoregulation with the greatest increase being seen at the coldest (20 °C) temperature. Second, we hypothesized that behaviors associated with a nest in the wild (i.e. nest building and sleeping) would be seen more frequently in contact with nesting material. Specifically, we predicted to see this difference in inactive and nesting behaviors. In cooler temperatures animals with a high surface area to volume ratio experience a high amount of heat loss (Dawson, 1967; Gordon et al., 1998; Gordon, 2004). Therefore, we predicted that nests would be more dome-like at cooler temperatures in order to counteract that heat loss.

2. Materials and methods

Many of the same materials and methods were used by Gaskill et al. (2009).

2.1. Animals and housing

A total of 48 C57BL/6J mice were purchased from Jackson Laboratories (Bar Harbor, ME, USA) at 26 days of age: 24 males and 24 females. Upon arrival the mice were randomly separated into same sex groups of three, ear notched for identification, and given one week to recuperate from shipping before testing began. The mice were housed in standard laboratory polycarbonate shoebox cages (Alternative Design, Siloam Springs, AR USA; 18.41 cm W × 29.21 cm D × 12.7 cm H) with aspen shaving bedding (Harlan Teklad, Madison, WI, USA) and wire cage lids from 4 to 12 weeks of age. The mice were kept on a 14:10 Light:Dark photoperiod (lights on at 06:00 AM), at 20 ± 1 °C with 60 ± 10% relative humidity and given food (Harlan Teklad, Madison, WI, USA; Mouse diet 2019) and water *ad libitum*. All housing and procedures associated with this experiment were approved by the Purdue Institutional Animal Care and Use Committee.

2.2. Thermal preference apparatus

We used three glass fish tanks (Fig. 1) as water baths to keep the mouse cages at a constant temperature. The water baths, heated by thermostatic electric fish tank heaters, were set to maintain constant ambient temperatures within the cages at 20 °C (a typical laboratory temperature), 25 °C (a temperature below the lower critical temperature; Gordon, 1993), or 30 °C (corresponding to the lower critical temperature as well as preferred ambient

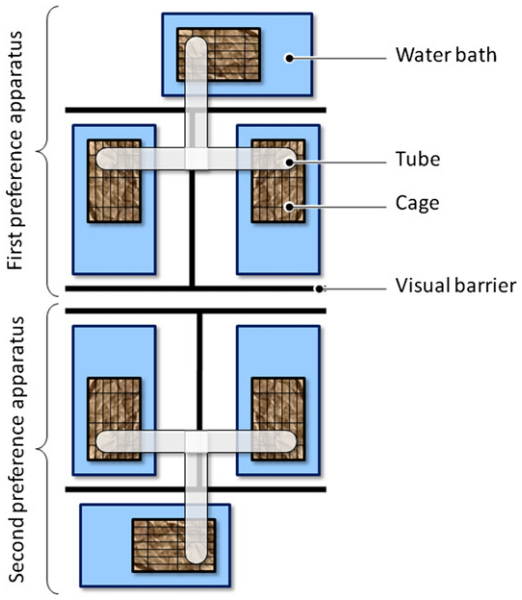

Fig. 1. Diagram showing the configuration of water baths and cages for testing cage temperature preferences for one group of male mice and one group of females simultaneously. The figure is reproduced with permission from Elsevier (Gaskill et al., 2009).

Fig. 2. Photograph of Eco-bedding nesting material.

temperature). Temperatures inside of each cage were confirmed prior to testing each day of the experiment by a thermometer just off the surface of the aspen bedding within the cage. Cages were of the same make and size as cages in which the mice were housed prior to experimentation. Approximately 0.64 cm of aspen bedding covered the floor of the cage and mice assigned to the nesting treatment received in addition 8 g Eco-bedding (Fig. 2; FiberCore, Cleveland, OH, USA) in all temperature options. Eco-bedding was chosen as the nesting treatment because it closely resembles materials used in the wild and is a material C57BL/6 mice (poor nest builders with commonly used compressed nesting material) can build with (Hess et al., 2008). *Ad libitum* food and water were located on top of all three cage lids within the experimental apparatus. The cages sat in a wire basket, immersed in the water baths up to 2.5 cm from the rim and secured with nylon straps that encompassed the water bath (Fig. 3). Hard plastic hamster tubing (S.A.M., Penn Plax Inc., Hauppauge, NY, USA) was used to connect the three cages together through holes in the cage lids. Tube ends