

Are feral house mice from the sub-Antarctic adapted to cold?

By P. I. WEBB, G. T. H. ELLISON, J. D. SKINNER, and R. J. VAN AARDE

Mammal Research Institute, University of Pretoria, Pretoria, South Africa.

*Receipt of Ms. 19. 06. 1996
Acceptance of Ms. 28. 09. 1996*

In small mammals adaptation to cold environments may be expressed in the form of elevated basal metabolic rate (BMR) (eg BUFFENSTEIN and JARVIS 1985), reduced minimum thermal conductance (eg CASEY et al. 1979), and/or elevated maximum non-shivering thermogenesis (NST) (eg HAIM and IZHAKI 1993). Marion Island (46° 54' S, 37° 45' E) lies in the sub-Antarctic and has one of the most oceanic climates in the world (SMITH and STEENKAMP 1990); mean surface air temperature is 5.7°C (SMITH and STEENKAMP 1990) while seasonal variation in mean surface air temperature is only about 4.1°C (SMITH 1987). House mice (*Mus musculus*) were introduced to Marion Island at least 170 years ago (BERRY et al. 1978), a time in which we might expect the passage of at least 300–400 generations. Such a period is certainly long enough for significant shifts in population genetics to occur. For example wild caught house mice bred for only 9 generations in the cold and then returned to a warm environment have been shown to be superior to controls in reproductive performance and growth (BARNETT et al. 1975). Also seasonal changes in heterozygosity in 3 out of 6 loci and genetic variation that was higher than expected for a small founder population have been taken as evidence for natural selection in an island population of house mice (BERRY and MURPHY 1970; BERRY and PETERS 1977) as has age related genetic variation in Marion Island mice (BERRY et al. 1973). Physiological parameters associated with thermoregulation have previously been shown to have low heritability (<0.1) in house mice (LACY and LYNCH 1979), lower for instance than body mass (circa 0.4) or aspects of thermoregulatory behaviour such as nesting (circa 0.3) (LACY and LYNCH 1979). Such differences in heritability are verified by the presence or absence of clinal variation in such parameters in the wild (LYNCH 1992). However it has been suggested that due to the harshness of the climate, *M. musculus* on Marion Island are living close to their physiological limit (BERRY et al. 1978) implying that selective pressure on thermoregulatory physiology in this population will be high. In this study we compare aspects of thermoregulatory physiology in adult *M. musculus* from Marion Island with allometric predictions from other murid and mammal species and with previous measures from other feral *M. musculus* populations and laboratory stocks. Our intention is to establish the presence or absence of adaptation of thermoregulatory physiology to the harsh Marion Island climate.

Feral adult *M. musculus* were live-trapped on Marion Island, maintained individually in cages in a climate chamber at the University of Pretoria and acclimated at constant temperature under a 12L:12D photoperiod for at least six weeks prior to the onset of experimentation. Food and water were available ad lib. Shredded tissue paper and sawdust were provided for bedding.

Standard metabolic rate (SMR) of individuals of known body mass was determined by measuring minimum oxygen consumption at 11 ambient temperatures ranging from 0 to 35°C using open-flow respirometry. At each temperature measurements were made on

five or six individuals randomly selected from a pool of 14 mice acclimated to 23 °C. SMR of a given mouse at a given ambient temperature was taken as the mean of the lowest five consecutive measures of oxygen consumption over a 2 hour period. At the end of the 2 hour period body temperature was taken by inserting a thermocouple 1 cm into the rectum. All measures of SMR were corrected to standard temperature and pressure of dry air. The thermoneutral zone was defined as the range of ambient temperature within which mean SMR (ie across all individuals) was minimal and independent of ambient temperature. Mean oxygen consumption within the thermoneutral zone was taken to represent basal metabolic rate (BMR). Thermal conductance was calculated as oxygen consumption during the last five minutes of the 2 hour measurement period divided by the body-ambient temperature differential. For each individual the lowest measure of thermal conductance at temperatures below the thermoneutral zone was taken to represent minimum thermal conductance. Maximum non-shivering thermogenesis (NST) was determined as maximum thermogenic response (oxygen consumption) to nor-adrenaline following the procedure of ELLISON and SKINNER (1991) in six mice acclimated to low temperature (5 °C) (HELDMAIER 1971). All measures of oxygen consumption were converted to Watts by assuming a calorific equivalence of oxygen of 20.1 W.ml⁻¹ (for a non-protein RQ of 0.8; ELIA and LIVESEY 1988).

Values of BMR, minimal thermal conductance and NST were compared with predictions from body mass based on allometric equations generated through log-log model I regression analysis of previously published data (Data used in regression analysis were as follows; BMR: 59 species of Muridae from HAYSEN and LACY 1985; Minimum thermal conductance: 19 species of Muridae from BRADLEY and DEEVERS 1980; NST: 25 species of Rodentia from HAIM and IZHAKI 1993). A measure was said to be significantly different to its predicted value if it fell outside the 95% confidence interval of the prediction.

BMR was significantly lower while minimum thermal conductance was exactly the same as the respective allometrically predicted values (Tab. 1). Once body mass differences had been accounted for by quoting all data as a proportion of allometrically predicted values, BMR also fell below that recorded in all laboratory populations of house mice and all other populations of feral house mice considered, although only marginally in the case of a feral population from Wisconsin (Tab. 1). Minimum thermal conductance also fell below that recorded in all laboratory or feral populations considered, although again the differences were marginal for two laboratory populations (Tab. 1). NST was significantly higher than the allometric prediction but was not consistently higher or lower than recorded in other populations of feral or laboratory house mice once differences in body mass had been accounted for (Tab. 1).

We therefore suggest that both BMR and minimum thermal conductance are comparatively low in *M. musculus* from Marion Island while NST is neither especially high or especially low. Low thermal conductance is consistent with genotypic or developmental adaptation to cold (CASEY et al. 1979) but low BMR is not. The lack of a comparatively high NST is consistent with previous analyses of body composition; even though interscapular brown fat mass (per gram body mass) increases with decreasing meteorological temperature across feral house mouse populations (JAKOBSEN 1981), Marion Island mice have comparatively less interscapular brown fat than do house mice from Taunton in the south of England, or even than house mice from Hawaii (BERRY et al. 1979). If *M. musculus* from Marion Island were physiologically adapted to cold we might expect them to demonstrate comparatively high NST.

However, low BMR is consistent with adaptation to limited food (and hence metabolisable energy) availability (McNAB 1986; WEBB and SKINNER 1996). Evidence that food availability is a limiting factor for *M. musculus* population expansion on Marion Island is circumstantial but implied by the coincidence of high mortality and declining food avail-

Table 1. Thermoregulatory physiological parameters in *Mus musculus*. BMR – basal metabolic rate. NST – non-shivering thermogenesis. Predicted values were calculated allometrically from log-log model I regressions of previously published data. See text for further details. Errors are ± 1 standard deviation. Measures are ranked in descending order by % of predicted value

| Parameter and reference | Population | Body mass (g) | Acclimation conditions (°C) | Value Measured | % predicted |
|---|---------------|--------------------|-----------------------------|-------------------------|-------------|
| BMR (Watts) | | | | | |
| GÓRECKI et al. (1990) | Poland | 13.2 | – | 0.364 | 214 |
| GÓRECKI and KANIA (1986) | laboratory | 27 | 20 | 0.513 | 184 |
| BARTKE and GÓRECKI (1968) | laboratory | 30 | ? | 0.536 | 179 |
| GÓRECKI et al. (1990) | Bulgaria | 18.6 | – | 0.274 | 128 |
| JAKOBSEN (1978) | Isle of May | 18.6 | summer | 0.225 | 104 |
| HELDMAIER (1971) | laboratory | 33.4 | 5 | 0.330 | 103 |
| RICHARDSON et al. (1994) | laboratory | 18.0 | 22 | 0.214 | 101 |
| HUDSON and SCOTT (1979) | laboratory | 45.5 | 20–24 | 0.373 | 94 |
| Richardson et al. (1994) | Wisconsin | 11.2 | 22 | 0.119 | 77 |
| Present study | Marion Island | 21.2 (± 4.2) | 23 | 0.171 (± 0.025) | 72 |
| Minimum thermal conductance (Watts. °C⁻¹) | | | | | |
| GÓRECKI and KANIA (1986) | laboratory | 27.9 | 20 | 0.0497 | 181 |
| JAKOBSEN (1978) | Isle of may | 18.6 | summer | 0.0268 | 121 |
| HUDSON and SCOTT (1979) | laboratory | 45.5 | 20–24 | 0.0381 | 107 |
| HART (1950) ^a | laboratory | 26 | ? | 0.0276 | 105 |
| Present study | Marion Island | 27.0 (± 3.4) | 23 | 0.0269 (± 0.0073) | 100 |
| NST (Watts) | | | | | |
| RICHARDSON et al. (1994) | Wisconsin | 11.5 | 22 | 0.886 | 399 |
| RICHARDSON et al. (1994) | Laboratory | 19.0 | 22 | 1.095 | 346 |
| Present study | Marion Island | 23.1 (± 4.0) | 5 | 1.136 (± 0.231) | 312 |
| HELDMAIER (1971) | Laboratory | 33.4 | 5 | 1.294 | 274 |
| JAKOBSEN (1978) | Isle of May | 18.6 | summer | 0.825 | 264 |

^a) in BRADLEY and DEEVERS (1985)

ability in winter (GLEESON and VAN RENSBURG 1982; MATTHEWSON et al. 1994). *Mus musculus* from Marion Island are also comparatively small (BERRY et al. 1978) although they are both heavier and have relatively shorter tails than feral house mice from Macquarie Island, also in the sub-Antarctic (BERRY et al. 1978). Small body size will help reduce total energy demand. Finally, incidental observations on house mice from Marion Island indicate a tendency to hoard food when available in excess both in the field (R. J. VAN AARDE, unpubl. data) and in the laboratory (G. T. H. ELLISON, unpubl. data). This may represent a behavioural adaptation to short term fluctuations in food availability in the wild.

We suggest that *M. musculus* from Marion Island do show physiological adaptation to cold (via a reduction in minimum thermal conductance) but that limited availability of energy on the island has prevented adaptive changes that would have resulted in increased in energy demand (eg increased BMR or NST).

Acknowledgements

Financial and logistic support were provided by the University of Pretoria and the Foundation for Research Development in South Africa. SARA FREARS commented constructively on an earlier draft of the manuscript.

References

- BARNETT, S. A.; MUNRO, K. M. H.; SMART, J. L.; STODDART, R. C. (1975): House mice bred for many generations in two environments. *J. Zool. (London)* **177**, 153–169.
- BARTKE, A.; GÓRECKI, A. (1968): Oxygen consumption by obese yellow mice and their normal littermates. *Am. J. Physiol.* **214**, 1250–1252.
- BERRY, R. J.; MURPHY, H. M. (1970): Biochemical genetics of an island population of the house mouse. *Proc. R. Soc., Series B* **176**, 87–103.
- BERRY, R. J.; PETERS, J. (1977): Heterogenous heterozygosities in *Mus musculus* populations. *Proc. R. Soc., Series B* **197**, 485–503.
- BERRY, R. J.; JAKOBSEN, M. E.; TRIGGS, G. S. (1973): Survival in wild-living house mice. *Mamm. Rev.* **3**, 46–57.
- BERRY, R. J.; PETERS, J.; AARDE, R. J. VAN (1978): Sub-antarctic house mice: colonization, survival and selection. *J. Zool. (London)* **184**, 127–141.
- BERRY, R. J.; BONNER, W. N.; PETERS, J. (1979): Natural selection in house mice (*Mus musculus*) from South Georgia (South Atlantic Ocean). *J. Zool. (London)* **189**, 385–398.
- BRADLEY, S. R.; DEEVERS, D. R. (1980): A re-examination of the relationship between thermal conductance and body weight in mammals. *Comp. Biochem. Physiol.* **65 A**, 465–476.
- BUFFENSTIEN, R.; JARVIS, J. U. M. (1985): Thermoregulation and metabolism in the smallest African gerbil, *Gerbillus pusillus*. *J. Zool. (London)* **205**, 107–121.
- CASEY, T. M.; WITHERS, P. C.; CASEY, K. K. (1979): Metabolic and respiratory responses of arctic mammals to ambient temperature during the summer. *Comp. Biochem. Physiol.* **64 A**, 331–341.
- ELIA, M.; LIVESY, G. (1988): Theory and validity of indirect calorimetry during net lipid synthesis. *Am. J. Clin. Nutr.* **47**, 591–607.
- ELLISON, G. T. H.; SKINNER, J. D. (1991): Thermoregulation and torpor in African woodland dormice, *Graphiurus murinus*, following cold acclimation. *Z. Säugetierkunde* **56**, 41–47.
- GLEESON, J. P.; RENSBERG, P. J. J. VAN (1982): Feeding ecology of the house mouse *Mus musculus* on Marion Island. *S. A. J. Ant. Res.* **12**, 34–39.
- GÓRECKI, A.; KANIA, Z. (1986): Maximum metabolism and thermoregulation in laboratory mice. *Acta Theriol.* **31**, 97–105.
- GÓRECKI, A.; MECZEVA, R.; PIS, T.; GERASIMOV, S.; WALKOWA, W. (1990): Geographical variation of thermoregulation in wild populations of *Mus musculus* and *Mus spretus*. *Acta Theriol.* **35**, 209–214.
- HAIM, A.; IZHAKI, I. (1993): The ecological significance of resting metabolic rate and non-shivering thermogenesis for rodents. *J. therm. Biol.* **18**, 71–81.
- HART, J. S. (1950): Interrelations of daily metabolic cycle, activity, and environmental temperature of mice. *Can. J. Res., Section D* **28**, 293–307.
- HAYSEN, V.; LACY, R. C. (1985): Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol.* **81 A**, 741–754.
- HELDMAIER, G. (1971): Zitterfreie Wärmebildung und Körpergröße bei Säugetieren. *Z. vergl. Physiologie* **73**, 222–248.
- HUDSON, J. W.; SCOTT, I. M. (1979): Daily torpor in the laboratory mouse, *Mus musculus* Var. Albino. *Physiol. Zool.* **52**, 205–218.
- JAKOBSEN, M. E. (1978): Winter acclimatization and survival of wild house mice. *J. Zool. (London)* **185**, 93–104.
- JAKOBSEN, M. E. (1981): Physiological adaptability: the response of the house mouse to variations in the environment. *Symp. Zool. Soc. Lond.* **47**, 301–335.
- LACY, R. C.; LYNCH, C. B. (1979): Quantitative genetic analysis of temperature regulation in *Mus musculus*. I. Partitioning of variance. *Genetics* **91**, 743–753.
- LYNCH, C. B. (1992): Clinal variation in cold adaptation in *Mus domesticus*: verification of predictions from laboratory populations. *Am. Nat.* **139**, 1219–1236.
- MATTHEWSON, D. C.; AARDE, R. J. VAN; SKINNER, J. D. (1994): Population biology of house mice (*Mus musculus* L.) on sub-Antarctic Marion Island. *S. A. J. Sci.* **29**, 99–106.
- M McNAB, B. K. (1986): The influence of food habits on the energetics of eutherian mammals. *Ecol. Monogr.* **56**, 1–19.
- RICHARDSON, C. S.; DOHM, M. R.; GARLAND, T. (1994): Metabolism and thermoregulation in crosses between wild and random-bred laboratory mice (*Mus domesticus*). *Physiol. Zool.* **67**, 944–975.
- SMITH, V. R. (1987): The environment and biota of Marion Island. *South African J.* **83**, 211–220.

- SMITH, V. R.; STEENKAMP, M. (1990): Climate change and its ecological implications at a sub-antarctic island. *Oecologia* **85**, 14–24.
- WEBB, P. I.; SKINNER, J. D. (1996): Physiological adaptation to aridity in the bushveld gerbil, *Tatera leucogaster*. *J. Zool. (London)* **238**, 693–701.

Authors' addresses: Dr. PETER I. WEBB, Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand; Dr. GEORGE T. H. ELLISON, School of Biological and Chemical Sciences, University of Greenwich, London SE18 6PF, UK; Prof. JOHN D. SKINNER and Prof. RUDI J. VAN AARDE, Mammal Research Institute, University of Pretoria, Pretoria 0002, South Africa.