

Letters to the Editors

Heat production and growth costs in the young rat

Coyer *et al.* (1987) gave male Sprague–Dawley rats weighing 103.5 g eight feeding treatments for 7 d. The treatments were four levels of feeding (4, 8 or 12 g/d and *ad lib.*) \times two feed nitrogen contents (26.6 and 10.8 g/kg). The rats were kept in single cages at 25°. Gains of protein and lipid were estimated by initial and final slaughter. The authors used the equation

$$\text{MEI} = \text{EpP} + \text{EfF} + \text{M} \quad (1)$$

to interpret their data. In this equation MEI is metabolizable energy intake, Ep and Ef are the partial energy costs of protein and fat respectively, P is protein deposition, F is fat deposition and M is maintenance. The energy retention (ER), which was estimated directly, can be subtracted from both sides of eqn (1) to give

$$\text{H} = \text{hpP} + \text{hfF} + \text{M}. \quad (2)$$

Eqn (1) is thus equivalent to making the assumption that all of the heat production (H), where $\text{H} = \text{MEI} - \text{ER}$, arises from three sources: protein retention (hpP), lipid retention (hfF) and M. The values of hp, hf and M can, in principle, be estimated from a suitable set of data.

Eqn (2) can be seen as the reduced form of a more general model:

$$\text{H} = \text{hpP} + \text{hfF} + \text{M} + \text{CT}, \quad (3)$$

where CT is the heat production of cold thermogenesis. In an environment that is thermally neutral, $\text{CT} = 0$ by definition and eqn (3) reduces to eqn (2). The use of eqn (1) by Coyer *et al.*, which is equivalent to eqn (2), carries with it the implicit assumption that the environment used was thermally neutral at all times for all of the rats on all of the treatments.

The effect of level of feeding on the temperature at which $\text{CT} = 0$ has been long appreciated (see Armsby, 1917, pp. 308–310). It would seem to be highly improbable that a temperature of 25°, as used by Coyer *et al.*, is thermally neutral both for rats which eat about 16 g/d when fed *ad lib.* and for rats given 4 g/d. If $\text{CT} = 0$ for the *ad lib.*-fed rats kept at 25°, it would be expected that CT would be positive, at least at some times of the day, for those given 4 g/d and 8 g/d and, perhaps, even for those given 12 g/d.

Where the animals on one, or more, of the treatments used are effectively cold the use of all of the data to estimate the values of Ep, Ef and M in eqn (1) will lead to meaningless conclusions. This would seem to be the case for the data of Coyer *et al.*

The assumption that rats of 103 g weight in single cages, given 4 g/d at 25° are effectively cold can be easily tested; if their heat production falls when the temperature is increased then they were cold at 25°.

To be able to use the data from a design of experiment such as that of Coyer *et al.* to estimate properly the values of Ep, Ef and M it would seem that the temperatures used for each treatment need to be different, i.e. to be thermally neutral at each of the feeding treatments used.

G. C. EMMANS

*East of Scotland College of Agriculture,
Animal Production Advisory and Development Department,
Bush Estate, Penicuik, Midlothian EH26 0QE*

Armsby, H. P. (1917). *The Nutrition of Farm Animals*. New York: Macmillan Publishing Co.
Coyer, P. A., Rivers, J. P. W. & Millward, D. J. (1987). *British Journal of Nutrition* **58**, 73–85.

Reply to letter by Emmans

We are grateful to Dr Emmans for his interest in our paper (Coyer *et al.* 1987). However, we do not agree with his critique and suggestion that our conclusions are meaningless. His review of basic animal energetics is unarguable, except that we see his eqn (3) as a specific case of a more general equation:

$$H = hpP + hfF + M + CT + DT,$$

where hp and hf are fixed costs for protein and fat deposition respectively, and DT is diet-induced thermogenesis. We define DT as all the extra heat production in response to food intake not included in the stoichiometries of fat and protein deposition. It is important that the possibilities of heat production of cold thermogenesis (CT) and DT are kept in mind in experiments of this kind, and a failure to consider either can lead to the kind of erroneous results which we review and discuss in our paper.

Emmans suggests that our animals were not at thermoneutrality and that we have confused CT with DT . We considered this but rejected it for the following reasons. First, if all animals were equally cold-stressed the effect of CT would result in a high value for maintenance (M), which we did not observe, and would not influence the estimate of growth costs. Second, in the more likely case that cold-stress increased at lower food intakes, this would decrease the apparent growth costs since the heat production associated with thermoregulatory thermogenesis at low food intakes would be replaced at increasing intakes by that associated with energy deposition. This results in high net efficiencies (see Close, 1978). Third, any attempt to increase environmental temperatures selectively in sub-groups of rats, as Emmans proposes, would give anomalous results since, according to Rothwell & Stock (1986), DT is suppressed when the ability to dissipate heat is impaired.

In any case the differences in heat production between our animals given the marginal- (MP) and high- (HP) protein diets were apparent in the *ad lib.*-fed animals as well as in those given lower energy intakes. In Fig. 1 we showed that *ad lib.*-fed MP animals gained less energy, despite a higher intake, than the *ad lib.*-fed HP group; while Fig. 2 showed that the higher heat production in the MP group was apparent when comparisons were made at any rate of protein gain. This is further evidence against the suggestion that CT was simply replacing reduced growth costs.

Thus any CT that may have occurred could not account for the changes which we observed and we can dismiss the suggestion that our results are meaningless. Rather we regard our work as confirming the original suggestion by Miller & Payne (1962) and confirmed by Gurr *et al.* (1980) that low-protein diets can be associated with increased heat production and that DT , as defined above, is an important factor to be considered in animal experiments; without taking this into account the determination of true partial efficiencies of fat and protein deposition is unlikely to be achieved. In any case Emmans' criticisms of our work is largely academic since, as argued by Millward *et al.* (1976) and Coyer *et al.* (1987), the factorial partitioning of heat production is only of value for the prediction of energy requirements under defined conditions, in which context constant-temperature designs have obvious practical relevance.

PENNY A. COYER, J. P. W. RIVERS and D. J. MILLWARD
Nutrition Research Unit, London School of Hygiene and
Tropical Medicine, 4 St Pancras Way, London NW1 2PE

Close, W. H. (1978). *British Journal of Nutrition* **40**, 433–438.

Coyer, P. A., Rivers, J. P. W. & Millward, D. J. (1987). *British Journal of Nutrition* **58**, 73–87.

Gurr, M. I., Mawson, R., Rothwell, N. J. & Stock, M. J. (1980). *Journal of Nutrition* **110**, 532–542.

Miller, D. S. & Payne, P. R. (1962). *Journal of Nutrition* **78**, 255–262.

Millward, D. J., Garlick, P. J. & Reeds, P. J. (1976). *Proceedings of the Nutrition Society* **35**, 339–349.

Rothwell, N. J. & Stock, M. J. (1986). *Metabolism* **35** (7), 657–660.