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Low protein feeding and energy transduction in rats

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Dear Editor-in-Chief:

The riddle in your inaugural editorial[1] is based on experiments by Andik[2] where 10 wk old rats were fed a chow containing 4.3% protein, as opposed to the normal 22%. One group of rats housed at room temperature (21 °C) failed to gain mass and died within 6 wk, while another group that were fed the same chow and housed at 5 °C gained mass and all survived.

The simple explanation is that the rats housed at 5 °C ate more of the low protein chow, driven by an appetite for energy, and so got closer to satisfying their protein demand, while the rats at 21 °C were protein deficient.

Behind that simple explanation is complex physiology, including thermal relations, appetite drives, the scaling effects of body size, and perhaps a new concept in animal ecology.

The outcome relies on consideration of the thermoneutral zone (TNZ), bounded at its lower end by the lower critical temperature (LCT). When an endothermic homeotherm is exposed to conditions below its LCT, the rate of heat loss (which is proportional to the temperature difference between the animal and the environment) exceeds the heat generation associated with the basal metabolic rate. To regulate body temperature the animal compensates for the increased heat loss by increasing metabolic heat production.

The increase in metabolism below the LCT requires fuel, and energy consumption increases. Animal producers know this relationship well. When a production animal is within its TNZ its productivity is optimal, because the animal can channel more ingested energy to growth (or other productivity like eggs or wool) and not "waste" energy on extra heat production.

Below the LCT the protein requirements do not increase, as long as energy intake is sufficient to meet energy demand.[3] If energy intake is insufficient, then gluconeogenesis is activated and protein requirements increase. When the rats at 5 °C consumed more food, driven by an energy appetite, their protein intake increased, and they were not as protein deficient as those eating less at 21 °C. The military knows these things, and the protein content of cold weather rations (8%) is significantly lower than normal rations (15%).[3]

The LCT is influenced by many factors, but two important ones are body size and insulation. The LCT for a naked, lean human is about 28 °C, so it might seem surprising that the LCT for a rat is also about 28 °C,[4] given that the rat is much smaller with a larger surface area to volume ratio (and so greater relative heat loss). The rat is advantaged in this respect by its fur. Adding a dressing of light clothing, the LCT of a human decreases to about 21 °C. That is probably why most animal houses are at about 21–22 °C, comfortable for lightly dressed humans. While 21 °C is below the LCT for a rat, 5 °C is well below the LCT and rats consume nearly twice as much energy at 5 °C compared with 21 °C.[2]

The interesting question is why do the rats not consume more food at 21 °C and thereby compensate for the lower protein content of the diet? When they are given a choice of diet, insects, fish, birds, and mammals will select a diet that satisfies their protein requirements.[5] But something happens when choice is constrained, as in the experiments of Andik et al.[2]

When the "protective" effect of cold exposure on low protein feeding was discovered, it was suggested that at 21 °C, the rats could not consume more of the low protein diet because they were limited in their ability to either store or dissipate extra ingested energy. Rats can be made to become obese, and they also have a system for dissipating excess energy via brown fat metabolism in the well-known process of diet-induced thermogenesis. So why did they not do either or both?

Indeed, the individual rats that tended to gain more adipose tissue did consume more low protein chow at 21 °C and so were less protein deficient, suggesting that a disposition toward obesity (which could be interpreted as an ability to over-consume energy) could "protect" from protein deficit. In addition, replacing sucrose energy with indigestible cellulose energy also led to an increase in protein intake, suggesting that the bulk handling of digesta was not the limit, but that dealing with extra digestible energy created a limit on intake.[6] It was hypothesized that the limit was an inability to dissipate the heat produced by diet-induced thermogenesis at 21 °C.

The notion that the ability to dissipate heat might set a limit on the amount of energy that a mammal can process has recently been developed into a new concept in ecology.[7] The limit on energy flow through ecosystems (including through mammals) has traditionally been viewed as a "supply side" problem, that is, the limit is set by how much energy an animal is capable of harvesting and processing in a given time. Speakman and Król argue that, at least in some situations, there will also be an expenditure side limit on energy flow, that is set by the ability of an animal to dissipate the heat load that is associated with the inherent inefficiency of energy

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transduction.[7] It could change the entire landscape of ecology if it turns out that heat loss ability sets a limit on how much of the energy that can potentially be harvested from an environment can be turned into new mammals.

Because 21 °C is below the LCT of an adult rat housed individually, as in the experiments of Andik et al.,[2] it is arguable whether the rats were unable to dissipate more energy as heat. At 21 °C the rats would have been eating more chow than if they had been exposed to > 28 °C. But it does not necessarily follow that a heat loss limit was not exceeded; 5 °C provides nearly double the temperature difference that 21 °C does. It is a reasonable prediction that rats housed at 28 °C and fed 4.3% protein would fail to thrive even more than the rats housed at 21 °C, and probably die sooner.

These are exciting times to be a thermal physiologist, not the least because the thermal world is changing. It is good to be reminded occasionally of seemingly simple, but ultimately profound, experimental results.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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