How rats economize

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CHAPTER 1

GENERAL INTRODUCTION

Adult animals, living in a constant biologically adequate environment, maintain a balance between energy uptake and energy expenditure. The energy store of the body does not fluctuate much, as the constancy of body weight and body composition shows, while the store is small in comparison to the daily energy turnover, especially in small animals. This can be achieved either by control of the uptake or the expenditure of energy.

That an animal adapts its uptake to the expenditure of energy is well known. Studies on this point were done by manipulating energy expenditure via a change of environmental temperature or via the amount of activity imposed on the animal. Cottle and Carlson (1954) increased the energy expenditure in rats by lowering the environmental temperature from 25^{o} C, a value in or close to the thermoneutral zone of these animals, to 5^{o} C. Animals placed in this cold environment ate twice as much as their controls in the warm environment. Mayer et al. (1954) exercised rats in a treadmill with a speed of one mile per hour. The animals practically doubled their food intake when the duration of exercise was increased from one to six hours per day, while body weight was maintained. The measured changes of food intake were representative for energy uptake because in adult rats important changes of digestion efficiency in relation to the level of food intake are never found (Nehring et al., 1959). In both experiments mentioned a balance between uptake and expenditure was reached again under the new circumstances as shown by the constancy of body weight during more than one week. Moreover, the size of the reserves was probably not influenced because this body weight had the normal value.

To conclude, an animal can change its energy uptake with at least a factor two for adapting it to the expenditure of energy.

The possibility that an animal adapts its expenditure to the uptake of energy is often called in question. Recently Le Magnen (1974) even stated that the control of energy expenditure is contrary to what body weight would require in view of hyperactivity in food deprivation and hypoactivity in obesity. Investigations on this point available in the literature involved either partial (Keys et al., 1950; Grande et al., 1958; Meyer and Clawson, 1964; Walker and Garrett, 1970), or complete (Cumming and Morrison, 1960; Kleiber, 1961; Morrison, 1968) food deprivation or, only in man, raising of intake by overfeeding (Miller and Mumford, 1967). In these experiments, contrary to those in which expenditure was manipulated, body weight did not remain at the equilibrium level for ad libitum conditions. A new balance between intake and expenditure was reached only sometimes (Keys et al., Walker and Garrett, l.c.). These facts complicate the interpretation of the results with respect to the question of *adaptation of expenditure to uptake*. Some metabolic savings will result from the mere fact that the underfed subject* has to handle and digest less food Moreover, during partial or complete deprivation, stored glycogen and fat or even parts of the cells themselves are used as fuel. Body mass will decrease, and this is bound to cause a drop in metabolism. However, following Cumming and Morrison (l.c.), I will not call these decreases 'adaptive'. Rather, I am inclined to restrict this term to the case where the underfed animal spends less free energy on a given function (e.g. protein turnover, or muscular effort for a given behaviour) than an ad libitum fed conspecific *of the same weight and body composition* would do (p.71). If this phenomenon could be shown to exist, a basis would thereby be laid for the view that evolution has provided the individual with a special capability of eking out its provisions in order to increase the chance that it may tide over temporary food scarcity, a condition

*This discussion emphasises the case of underfeeding, since this is the only condition used in my experiments. An analogous definition of 'adaptation of expenditure to uptake' can be formulated for the case of overfeeding.

common in the natural habitat of many species. However, such a definition of adaptive restriction of expenditure involves formidable operational difficulties. I shall return to some aspects of this problems in chapter 8. For the moment it will suffice to state that conclusions in the literature are not unanimous as to the question whether or not changes in metabolism caused by manipulation of food intake, can be accounted for exclusively in terms of changed body mass and cessation of food processing. Cumming and Morrison (1960) state: 'The total energy expenditure of the rats fell during the 48 hr fast and rose during refeeding. When the changes in body weight and food intake were allowed for, the metabolic rate was found to remain constant throughout the whole experimental period'. In contrast, Walker and Garrett (1970) conclude that even after correction for body size reduction 'the energy expenditure declined markedly as the period of undernutrition was prolonged'. (They did not take into account changed costs of food processing, but this effect will be constant from about the second day onwards, whereas the decrease continued beyond that time.)

The present study is a contribution to the further analysis of the problem of adaptation of energy expenditure to uptake. Clearly, this can not be solved by the study of total metabolic rate alone, but only by an analysis of the various components that make up this total. Customarily four components are distinguished in the energy metabolism of a homeotherm (Gessaman, 1973): basal metabolism; metabolism above the basal level which is used for thermoregulation; metabolism associated with activity; and metabolic processes involved in the digestion of food. I shall use the same division. However, it should be pointed out that what I can measure in my experiments is not the rate of energy expenditure e.g. on the process of performing muscular activity, but only the difference in metabolic rate between the period during which that activity takes place and periods in which the animal is not engaged in muscular activity. This difference gives the cost of activity only if the other components of energy expenditure (digestion and other processes in resting metabolism) proceed at the same rate irrespective of the occurrence of muscular activity. I have no means of ascertaining whether this is so, but it seems highly doubtful for instance in view of the effects of sympathetic discharge and adrenomedullary secretion causing splanchnic vascular constriction, inhibition of lipogenesis, etc. In principle therefore I can state only the difference in metabolic rate between the following *conditions*: 1) animal resting in the post absorptive state, 2) animal resting and processing food, 3) animal active. For brevity, however, I shall discuss my results in terms of a resting, a food processing, and an activity *component* of metabolism ((see also p.65). The possible influence of the demands of thermoregulation on metabolic rate could be studied in principle by making observations at different ambient temperatures. For instance if the animal is placed in the cold, this should lead to an increase in one or more of the other three components of metabolism. Such temperature experiments, however, fell outside the scope of the present study.

The laboratory rat was chosen as the subject of my experiments because it is commonly used in studies on caloric regulation. Intake was changed in one direction only, namely reduction. All experiments were done at the same temperature in the thermoneutral zone of the rats for two reasons. First, I wished to avoid the complication of special (and not directly measurable) heat production for thermoregulation. Second, experiments with food deprived animals can be continued longer without lethal effects, for at temperatures in or near the thermoneutral zone animals can mobilize more of their energy stores as shown by data on birds (Kendeigh, 1945) and rats (Kleiber, 1945) starved till death at different temperatures. Consequently in my experiments, notwithstanding long periods of food deprivation, only two out of more than one hundred animals died; the others could be refed.

The energy expenditure was measured by tw methods: 1) a balance technique (chapter 3), calculating expenditure from food intake, faeces production and changes in body reserves, and 2) indirect calorimetry, calculating expenditure from the gas exchange of the animals (chapters

4-7). By increasing the temporal resolution of the latter method and combining it with other techniques a detailed analysis of total expenditure into its components was made possible. This procedure will be described in detail in chapter 2.

I first determined the change in total expenditure during food deprivation (chapter 3). This change was further analysed in terms of the energetic consequences of: 1) the cessation of food processing (chapter 4); 2) changes of activity (chapter 5); and 3) changes of fasting resting metabolic rate (chapter 6). Finally the consequences of the expenditure changes for regulation of body temperature were studied (chapter 7). With respect to the first point it is regrettable that the energy expenditure on feeding behaviour could not be separated from that on other behaviour. Therefore my estimate of the energy expenditure associated with food processing included only the costs of internal processing, while for instance food handling was measured together with the costs of non-feeding behaviour.