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# Self-Starvation in the Rat: Running versus Eating

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Rats given the combination of unrestricted access to an activity wheel and restricted access to food can lose weight to the extent that they will die unless removed from these conditions. Although this has been known for forty years, why this happens has remained unclear. The phenomenon is paradoxical in that one might expect such rats to eat more as their weight decreases, but in fact they eat less than resting controls. This lecture first examines some of the factors than influence whether self-starvation will occur, such as age, time of food access, type of food and ambient temperature. It then compares competing explanations such as circadian adaptation, thermo-regulation and food aversion learning. As so often in psychology, it turns out that self-starvation results from a combination of many separate factors. The general implications of this research are examined, including whether it provides a useful animal model for human anorexia nervosa.
*Keywords: self-starvation, rats, anorexia nervosa*

Las ratas sometidas simultáneamente a restricción de comida y acceso a una rueda de actividad pierden peso hasta el extremo de morir si no son retiradas a tiempo de estas condiciones. Aunque este hecho es conocido desde hace cuarenta años, la razón por la cual esto sucede permanece sin resolver. Lo paradójico de este fenómeno reside en que, aunque sería esperable que las ratas comiesen más a medida que su peso disminuye, en realidad estos animales comen menos que sus controles sedentarios. En esta conferencia se examina, en primer lugar, algunos factores que influyen en el desarrollo de la auto-inanición como son la edad, el tiempo de acceso a la comida, el tipo de comida y la temperatura ambiental. A continuación se comparan algunas explicaciones tales como la adaptación del ritmo circadiano, la termorregulación y la aversión adquirida a la comida. Tal como ocurre con frecuencia en psicología, la auto-inanición es el resultado de diferentes factores. Finalmente, se examinarán algunas implicaciones más generales de esta investigación, incluida su posible utilidad como modelo animal para el estudio de la anorexia nerviosa en humanos.
*Palabras clave: auto-inanición, ratas, anorexia nerviosa*

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## Historical Background

Richter is sometimes known as the "father of the biological clock" for his pioneering research on biological rhythms that started in the 1920s and continued for some decades (Richter, 1922; Schulkin, 2005). Much of this research used a simple piece of equipment, the activity wheel, which has remained essentially unchanged ever since. The standard (Wahmann) type consists of a round drum made of a metal frame and mesh, with a diameter of about 330 mm so that each complete revolution made by a rat walking or running inside corresponds to a distance of about 1.1 m. Attached to the wheel is a side cage with a door that leads to the wheel. Under *open wheel* conditions, an animal can move freely between wheel and cage, whereas under *closed wheel* conditions, an animal is confined to the wheel by shutting the door.

A basic finding made by Richter (1922) was that for rats living in an open wheel condition, when and how much they run is subject to a diurnal rhythm: The nocturnal rat runs a great deal at night, but little during daylight hours. What was discovered much later is that running can also become subject to an independent biological clock set by when food is made available. If access to food is restricted to a few hours at a regular time each day, a rat will come to run increasingly during the preceding 3-4 hr period (*food anticipatory period;* FAP) even if this is during the daytime (e.g., Mistlberger, 1994).

Another factor that determines how much a rat will run is weight loss: A rat with restricted access to food runs much more than one with unrestricted access. The relationship between weight loss and activity was very important for Hull's concept of *general drive* that was central to his theory of motivation (Hull, 1943). A large number of experiments were run in the 1950s and early 1960s to test this theory, as reviewed in Bolles' influential 1967 book, *Theory of Motivation.* Many of these experiments measured rates of running as a function of various kinds of food deprivation schedules and, when the experiments were reported, the authors noted—often only in a footnote—that a surprisingly large proportion of rats died in the course of the experiment (e.g., Hall & Hanford, 1954; Bolles & de Lorge, 1962). That this might be of interest in its own right, and not just a distressing side effect, was first noted by Spear and Hill (1962), followed up by Routtenberg and Kuznesov (1967), who were the first to carry out a systematic study of what they named *self starvation* in the rat.

In what became a standard procedure, Routtenberg and Kuznesov (1967, Experiment 3) introduced rats simultaneously to a feeding schedule that restricted access to food to 1 hr per day and to life in an open wheel. They found that the rats' weights dropped steadily over a 14-day period, by which time all ten had to be removed. Loss of weight was accompanied by ever more intense running (see Figure 1). Six years later, Paré and Houser (1973) drew further attention to the phenomenon with their report that, when rats subjected to this procedure—one they referred to as *activity stress*—

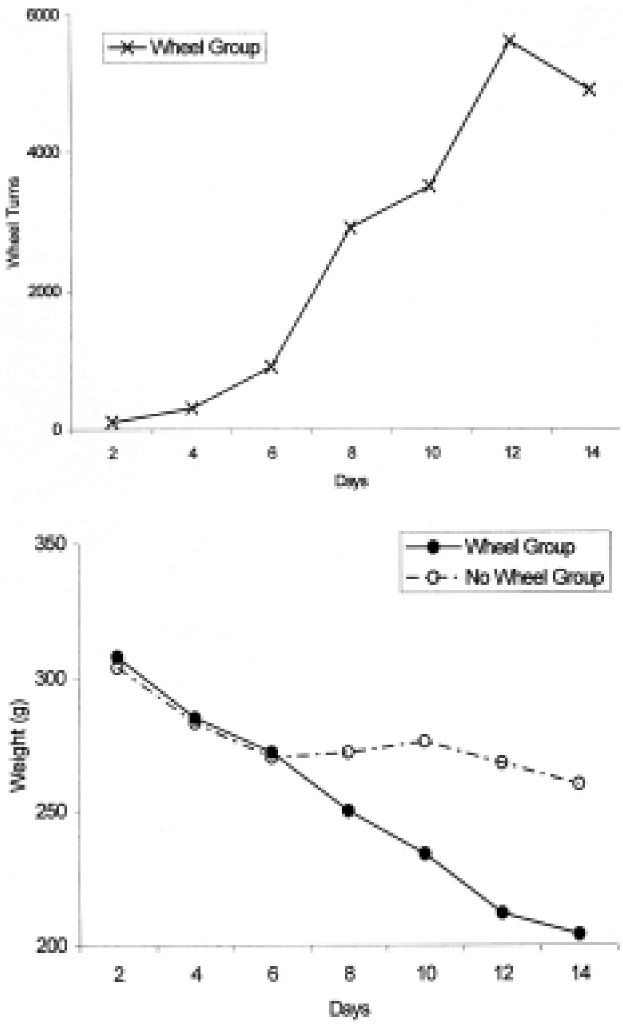


*Figure 1.* Decreases in body weight in a group of rats exposed to an ABA procedure (Wheel group) and in resting controls simply restricted to 1-hr per day feeding (No wheel group). Also shown is the increasing rate of wheel turning by the Wheel group. Redrawn from Routtenberg and Kuznesov (1967, Figure 4).

lost 30% or more of their body weight, they developed stomach ulcers. Over the next fifteen years or so, Paré and his colleagues continued a productive research program on the phenomenon. However, the general impact of this work was reduced as interest in the relation between stress and ulcers in humans declined with the discovery that a bacterium causes most human gastric ulcers (Marshall & Warren, 1984). Meanwhile, the term *activity-based anorexia* was introduced by Epling, Pierce, and Stefan (1983) as a label for running-based weight loss.

Given the variety of labels and the potential confusion between a procedure and an outcome, in our research we have used the term *activity-based anorexia* (ABA) to describe the procedure introduced by Routtenberg and Kuznesof (1967) and the term they used, *self starvation,* to describe the outcome for many rats subjected to this procedure, namely, progressive weight loss that can be halted only by removing the ABA conditions. Our experiments normally give rats a 90-min period of food access each day and employ a removal criterion whereby a rat is removed from the conditions once its weight declines to 75% or less of its initial weight on two successive days. This is in time to prevent the onset of ulceration and, once given unrestricted access to food, our rats soon recover weight and remain healthy.

## Factors Affecting Self-Starvation

A great deal is now known about the factors influencing whether a rat will self-starve (for a comprehensive set of references, see Gutiérrez, Vazquez, & Boakes, 2002). Subject characteristics are particularly important. Most notably, the effect is much stronger in younger rats (Woods & Routtenberg, 1971). Other factors of this kind include pre-experimental experience such as environmental enrichment and prior stress. For example, we have found that rats given brief handling when pups, as a result, receive more maternal interaction, and lose weight more slowly when subjected to an ABA procedure several weeks later (Carrera, Gutiérrez, & Boakes, 2006).

Variations in the ABA procedure can also be important. Thus, as might be readily predicted, the longer the feeding period, the slower the weight loss and the less likely that self-starvation will occur; a similar effect is obtained by reducing the time per day that a rat can spend in the wheel. Less obviously, rate of weight loss is also reduced by giving two feeding periods per day of the same total duration as a single period and by providing access to food during the dark cycle instead of well into the light cycle, as is much more common. A further factor that has been of recent interest to us is ambient temperature: Most ABA experiments have been run at a similar temperature to that in the colony room, usually in the range 20-22 degrees. When the temperature is raised to around 30 degrees, rats introduced to the ABA procedure run less and lose weight more slowly (Gutiérrez, Baysari, Carrera, Whitford, & Boakes, 2006). Other factors that influence whether self-starvation is likely to occur are discussed in the following sections where I review possible explanations of the phenomenon.

## What Makes a Rat Run?

A striking aspect of a rat's behaviour when introduced to an ABA procedure is the rapid increase in running that occurs. It is not uncommon for rats to turn the wheel up to 10,000 times per day within a few days, an amount equivalent to running 11 km. Thus, one of the key questions towards understanding self-starvation is why do rats run, especially when deprived of food? The other is: What processes give rise to the relationship between running and weight loss? I will return to this question in the following section.

Rats are not exceptional with respect to running in a wheel. In a landmark review, Sherwin (1998) concluded that almost all species tested have shown spontaneous running in an activity wheel. He suggested that an important factor is self-reinforcement provided by the vestibular and other feedback stimulation produced by running in a wheel. Just think of young children on swings or roundabouts. This may perhaps produce the endorphins that some authors (e.g., Epling & Pierce, 1992) have suggested provide the basis for conditioning of a place preference when a rat is repeatedly placed in a distinctive chamber after a session in an activity wheel (Lett, Grant, Byrne, & Koh, 2000) or of a flavour preference if a novel flavour is provided after a wheel session (Hughes & Boakes, in press).

On the other hand, running by rats is unusual in its sensitivity to both food deprivation and anticipation of food. When groups of rats are deprived to different degrees of body weight loss and are then given access to a wheel, the amount they run is a monotonic function of deprivation (see Figure 2). In contrast, some rodent species show decreases in running with food deprivation (Sherwin, 1998). Following Bolles' (1970) analysis of defensive reactions to threat, initial wheel running by a hungry rat can be seen as a *species-specific hunger reaction* (Boakes, 1997), behaviour that is subsequently strengthened by self-reinforcement.

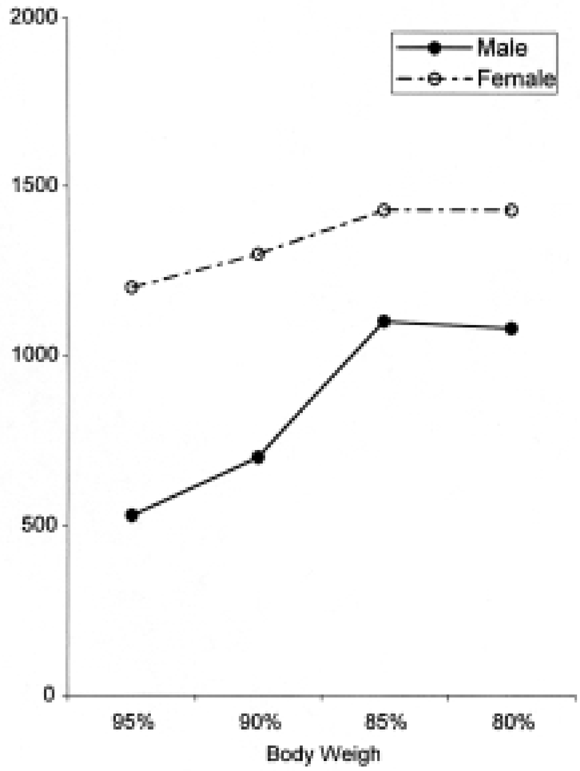


*Figure 2.* Running as a function of weight loss. Daily food access was adjusted so as to produce target levels of weight loss in the eight groups prior to giving them 1-hr wheel access on four successive days. The data points represent means over these four sessions. Redrawn from Boakes, Mills and Single (1999, Figure 4).

## How is Running Related to Loss of Body Weight?

The high level of running seen especially in young rats can suggest that a rat's weight loss is a direct result of the excessive energy consumed by this vigorous activity. However, activity-based calorie loss is not normally a major cause of weight loss. Thus, rats with free access to food run at a much lower rate if given 2-hr wheel access per day than if given 24-hr access, and yet weight loss in the two groups does not differ (Lattanzio & Eikelboom, 2003). At least two pieces of evidence from my laboratory point to the same conclusion for food-deprived rats. One is the finding that, when given wet mash in an ABA procedure, eight rats ran just as much as controls given dry food. However, none reached the removal criterion, whereas 6 out of the 8 rats given dry food did so (Boakes & Juraskova, 2001). Further evidence comes from an experiment in which a group of rats was placed on the feeding schedule for two weeks ahead of being placed in the wheel. These rats ran much more as soon as they were placed in the wheel than a control group given food restriction and placement in the wheel at the same time, as in the standard ABA procedure. Importantly, despite their high rate of running, the pre-adapted group lost weight more slowly than the control group (Dwyer & Boakes, 1997).

The above experiment was based on the idea that rats lose weight in the ABA procedure because running in some way retards their adaptation to a restricted daytime feeding schedule (Kanarek & Collier, 1979). When a rat that normally eats a number of meals each night and sleeps much of the day is given access to food for, say, 90 min in the middle of the day, it eats very little at first and as a consequence loses weight. Even rats without access to a wheel can take up to two weeks before the amount they consume in these 90 minutes reaches an asymptote and their body weight recovers. When we measured the food intake in the above experiment, it turned out that the pre-adapted rats ate almost twice as much as the control group from the time both groups were given access to the wheels and this difference was maintained for the next two weeks until rats from the control group started to reach the removal criterion. This result and related findings, such as the absence of self-starvation in a group given food at a time—the start of the dark period—when the rats normally ate, persuaded us that the key factor in ABA-induced weight loss is not running per se, but the decrease in food intake and that one reason this decreases is because rats are only slowly adjusting to eating at what, for a rat, is an abnormal time of day (Dwyer & Boakes, 1997).

As in almost all other ABA experiments, the food available to the rats in our early experiments was the same dry chow they had had throughout their lives. This suggested that dehydration might play a role, even though a rat in a standard ABA procedure can drink water at any time from a bottle protruding into its side cage. On measuring how much rats drank from this bottle, we found that the more they ran, the less they drank, especially during the FAP. In contrast, compared to rested controls, rats that had been running drank more during the feeding period. These data suggested that decreased intake of dry chow during the limited feeding period might reflect both the reduced palatability of this food to a somewhat dehydrated rat and satiety signals from a stomach full of water. Supporting evidence came from the experiment described earlier in which self-starvation was prevented by the use of wet mash in the ABA procedure (Boakes & Juraskova, 2001).

This dehydration account suggests that, as a rat runs increasingly from one day to the next, the difference between how much it eats and how much a resting control rat eats during the 1-2 hr period that follows should become progressively wider. This is rarely seen in our ABA experiments, thus suggesting that dehydration may be a minor factor. Particularly puzzling was the finding in these and other experiments that the difference in food intakes between wheel and resting groups could appear after the first 22.5-hr session in the wheels, when the rats had run little during this time compared to the amounts in subsequent days (Boakes & Juraskova, 2001; see Figure 3). (We would have been less surprised if we had paid closer attention to Routtenberg and Kuznesof's 1967 report).

A possible solution arose from Lett and Grant's (1996) discovery that rats will acquire an aversion to a novel taste presented prior to each of three 30-min periods in a closed activity wheel. Since then, conditioned taste aversions based on running—and also on swimming—have been extensively documented under a range of conditions (Boakes & Nakajima, in press). However, various studies have indicated that, whereas rats with access to a wheel readily acquire an aversion to a novel food, a very familiar food like dry chow does not become aversive (Baysari & Boakes, 2004; Satvat & Eikelboom, 2006; Sparkes, Grant, & Lett, 2003). Nevertheless, there remains the likely possibility that, whatever internal state produced by a rat's initial encounter with a wheel serves as an unconditioned stimulus to support food aversion learning, the same state acts to suppress food intake. This activity-induced state may last several hours, at least in non-deprived rats (Lattanzio & Eikelboom, 2003).

A final hypothesis about the relationship between running and weight loss is based on the principle of thermoregulation. Most rat colonies are maintained at an ambient temperature in the range 20-22 degrees. This presents no challenge to a rat's defence of its core body temperature of around 27 degrees, especially if it is housed with other rats. It is when a rat loses weight that the challenge begins. When given a choice of positions along a graded temperature space, the greater their loss of weight, the warmer the position a rat chooses (Sakurada et al., 2000). Thus, as a rat loses weight under ABA conditions in a cool laboratory, its core temperature is under increasing threat, but periods of vigorous running are followed by increases in body

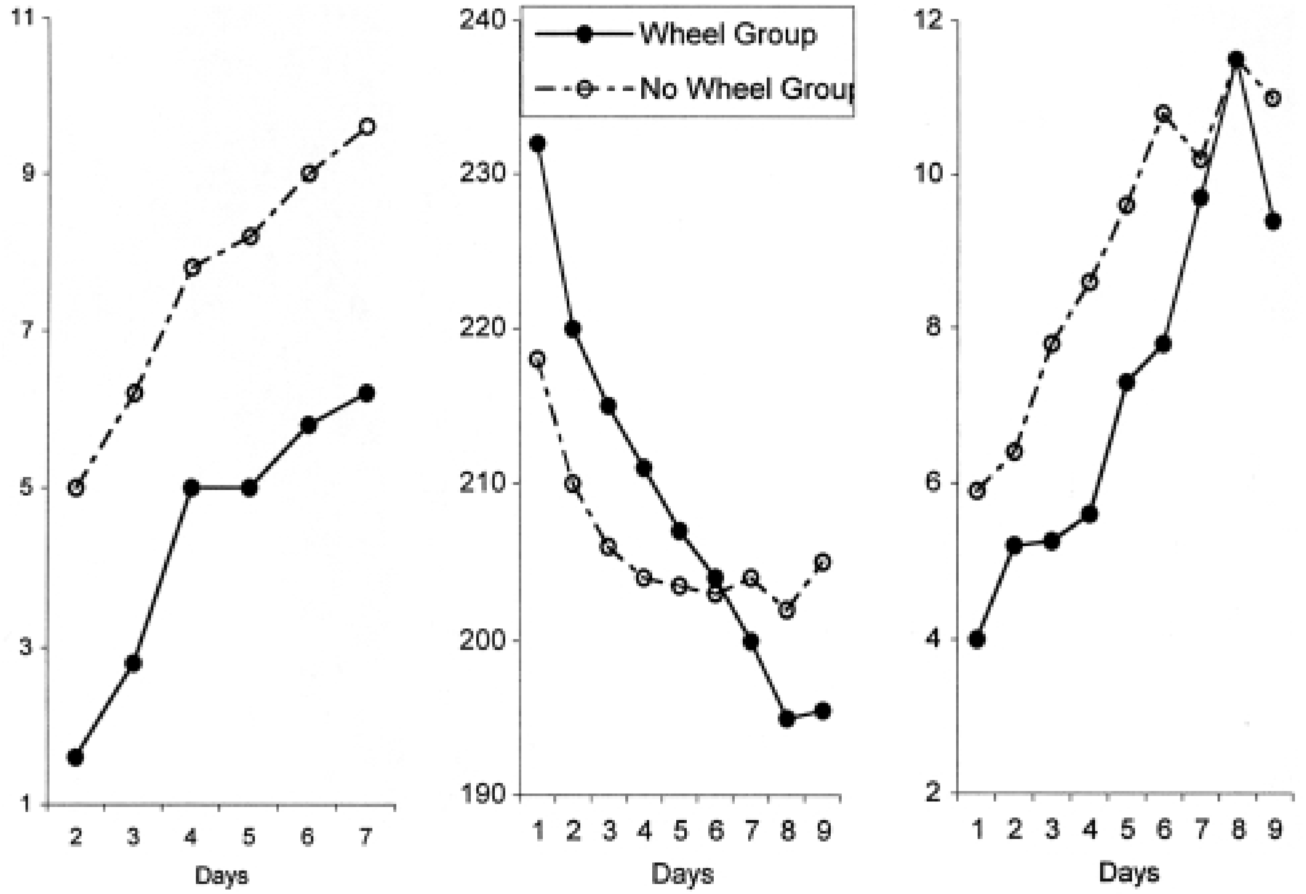


*Figure 3.* Food intake in rats exposed to ABA procedures (Wheel groups) compared with that of rats given the same feeding schedule but no access to wheels (No wheel groups). The left-hand panel shows two groups from Routtenberg and Kuznesov (1967, redrawn from the right-hand panel of their Figure 2) given 1-hr daily food access. The middle panel shows weight changes in the Wheel and No wheel groups from Boakes and Juraskova (2001, Experiment 1, redrawn from Figure 1). The right-hand panel shows the daily food intakes from the same two groups.

temperature (Hillebrand, de Rijke, Brakkee, Kas, & Adan, 2005). According to one version of the thermoregulation hypothesis, running is reinforced by such temperature increases in what is ultimately a self-defeating strategy (Gutiérrez et al., 2006; Lambert, 1993). This cannot be the only reason for running, since rats will still run when the ambient temperature is above their thermoneutral level and the rat needs to lose, rather than generate, heat (e.g., Campbell & Lynch, 1968). To what extent thermoregulation contributes to the self-starvation effect is unclear. In my view—but perhaps not that of my Santiago colleagues—a serious weakness of this hypothesis is that it makes no reference to the central paradox of the self-starvation effect: that ABA rats need more food, yet eat less, than resting controls. A variant of the hypothesis that was first tested and rejected by Routtenberg and Kuznesof (1967) proposes that running increases body temperature and this produces satiety signals to reduce food intake. Interestingly, when comparing rats run at a neutral (21 degrees) and a high (29 degrees) ambient temperature, we found no difference in intake during a 90-min feeding period, but more rapid weight loss at the neutral temperature (Gutiérrez et al., 2006).

When put together, supporting evidence for most of the above hypotheses suggests that self-starvation does not result from a single process, but reflects a combination of factors whose relative importance is difficult to establish and doubtless varies across conditions. Nonetheless, the standard ABA procedure first introduced by Routtenberg and Kuznesof (1967)—suddenly restricting rats at least 70 days old to 1-2-hr of familiar food at a fixed time each day and at the same time giving them unrestricted access to a relatively unfamiliar activity wheel in an ambient temperature of 20-22 degrees—appears to produce self-starvation in many rats for the following main reasons. Early experience of the activity wheel induces a state—one that supports acquisition of an aversion to a relatively novel taste—that suppresses eating for a period following the activity. Recovery of food intake to the same level as that of resting controls is hindered by the increase in running resulting from the steady decrease in an ABA rat's body weight.

Because the rat is eating less, it is slower than resting controls to adapt to eating enough in 1-2 hr at an unusual time of day for its body weight to start to recover. If increase in food intake occurs too slowly, the rat's weight will continue to fall.

## How is Self-Starvation in the Rat Related to Anorexia Nervosa?

One way of summarizing the above experiments with rats is to list risk factors for the development of self-starvation when a rat has access to an activity wheel. These include in approximately decreasing order of importance: sudden introduction of restricted feeding, youth, cool ambient temperature, and eating relatively unpalatable food soon after exercising. Some of these factors are similar to those for human anorexia nervosa, thus supporting the connection between this disorder and the rat phenomenon, a connection first examined extensively by Epling and Pierce (1992). But first, to note the obvious differences. While the experimenter imposes food restriction on a rat, an anorexic's diet restriction is self-imposed. The social, cultural, or professional reasons for this are clearly never going to be illuminated by any animal model. Furthermore, after a rat has lost considerable weight as a result of several days exposure to an ABA procedure, if wheel access is now denied or access to food no longer restricted, food intake can increase rapidly and body weight recover to a normal level within a few days (Boakes, Mills, & Single, 1999; Epling & Pierce, 1992).

On the other hand, there are some strong similarities between self-starvation in the rat and anorexia nervosa. In most cases of what has been labelled *activity anorexia* the onset of the disorder can be linked to the patient's adoption of a restricted diet at the same time as embarking on a programme of vigorous exercise (Epling & Pierce, 1992, 1996). Furthermore, in many cases of anorexia in which there does not appear at the onset of the disorder to have been adoption of an unusual level of exercise, a common symptom noted when considerable weight loss has occurred is a high level of physical activity or, at least, a pervasive restlessness (Gutiérrez et al., 2002). Although running in an activity wheel or on a voluntary treadmill (Collier, 1969) may be a species-specific hunger reaction in the rat, there is no specific activity that serves as an innate human reaction to body weight loss. This does not mean that humans cannot develop particular habitual activities—for example, jogging or running up stairs instead of taking the lift—whose intensities may well be dependent on weight loss in a similar manner to running in the rat. Such activities have conventionally been seen as reflecting a wilful strategy to burn up calories and, although this may often be how they start, it seems that the behaviour can become autonomous and controlled more by "biology" than by conscious decision-making.

The usefulness of an animal model of some human disorder depends on whether it can suggest effective treatment. In addition to lifting food restriction or denying access to a wheel, increasing the ambient temperature can retard an ABA rat's weight loss or even increase it (Gutiérrez et al, 2006; Gutiérrez, Cerrato, Carrera, & Vazquez, 2007). Given the notorious difficulty of persuading anorexic patients to eat more and exercise less, the effectiveness of keeping anorexics warm as an important element in therapy is currently under evaluation in clinical trials (e.g., Birmingham, Gutiérrez, Jonat, & Beumont, 2004).

In public health terms, a currently far more serious eating disorder than anorexia is obesity. The most pertinent experiment of those reviewed here is one that gave rats access to an activity wheel while maintaining their unrestricted access to food and water. As noted briefly above, Lattanzio and Eikelboom (2003) compared rats given either 2-hr or 24-hr wheel access with a no wheel group. Their unexpected finding was that 2 hr per day in an activity wheel reduced food intake and maintained lower body weights than those of rats without a wheel to exactly the same extent as 24-hr access to a wheel. Public health campaigns are being introduced in many developed countries to combat the current obesity epidemic. If these are successful in persuading their citizens—particularly the younger ones—to introduce more physical activity into their lives, any consequent impact on body weight will result, not from the calories burnt up, but from the as yet poorly understood activity-produced state that underlies the paradox whereby even a limited amount of exercise can reduce how much food rats and people eat.

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