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RESTRICTION OF WHEEL RUNNING AND SELF-STARVATION IN RATS

by

BARBARA JOAN KNOLL MCKENZIE

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Supervisor

Date: Spring 1983

DEDICATION

To Frank Epling and David Pierce for demanding the perseverance and quality of work necessary to complete this research.

ABSTRACT

This study investigated limited activity wheel access and self-starvation in rats. Rats on 1 hour daily food were allowed 0, 2, 6, 12, or 23 hours daily wheel access. Despite no or limited wheel access, control and 2 hour groups suffered marked weight loss; this unexpected finding was attributed to inadequate daily food presentation. Rats in the 6 hour and 23 hour groups self-starved, manifesting declining food intake with rapid, severe weight loss and a high rate and net amount of wheel running. The 12 hour group maintained relatively high food intake and therefore did not self-starve. It was concluded that a very high rate of running for moderate duration (6 hour group) exerts the same suppressing effect on food intake as a moderate rate of running for prolonged duration (23 hour group). Intensity of exercise was identified as an important variable in self-starvation in rats and also implicated as a potential area of research for human weight disorders (anorexia nervosa and obesity).

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

Research has implicated a reciprocal interaction between restricted food and increased physical activity as a precipitating factor of self-starvation in rats (Routtenberg and Kuznesof, 1967; Routtenberg, 1968; Epling, Pierce and Stefan, 1981). This research may also suggest factors for the development of human anorexia nervosa (Epling et. al., 1981). The present study was conducted to determine the effects of limiting opportunity to activity on rats given restricted food. More specifically, it was recognized that limiting access to activity could exert either of two influences on self-starvation in rats. First, self-starvation might be depressed or eliminated since net amount of exercise would also be limited. However, to the extent that restricted food promotes activity, a second potential influence was that rats would respond to limited activity access by adopting a high rate of exercise, thereby remaining susceptible to self-starvation.

Epling and his associates (1981) used a factorial design to investigate restricted food and physical activity in rats. In order to provide cross-species generality for findings, a parallel experiment using mice was also conducted. Included in the design were two levels of food availability (free food or 1 hour daily food access) and two levels of activity wheel access (no access or free access except during food presentation). Animals were assigned to one of four conditions:

free food and no wheel access; free food and free wheel access; 1 hour daily food and no wheel access; 1 hour daily food and free wheel access. The criterion for weight stabilization was body weight on Day 4 of any 4 day period equal to or exceeding that on Day 1. Results showed that all animals (except one mouse) in the first three conditions stabilized weight. The fourth condition (1 hour daily food and free wheel) was unique in that animals self-starved. Although animals in this condition initially showed increases in food intake and moderate activity levels, they subsequently became more active, decreased food intake and suffered severe weight loss. This paradoxical relationship between food intake, wheel running and weight loss was so extreme that animals were removed from the experiment at 70% of their pre-experimental weight to prevent their death.

Epling et. al. (1981) attribute self-starvation to restricted food which they hypothesize generates increased activity (i.e. wheel running) in a matter analagous to the development of schedule-induced behavior (e.g. Falk, 1971; Staddon and Simmelhag, 1971). Presumably, this increased activity, generated by restricted food, leads to decreased food ingestion; decreased ingestion then stimulates even higher activity levels.

The self-starvation effect was also documented by Routtenberg and Kuznesof (1967) in a four part study on starvation in rats. Their first experiment investigated weight stabilization and restricted food. All subjects were fed for 30 minutes per day. Control rats were housed in standard cages and experimental rats in cages with activity wheels. Experimental rats were placed in one of four conditions: no

wheel access 1 hour prior to feeding: no wheel access 2 hours prior; no wheel acess 1 hour subsequent to feeding; no wheel access 2 hours subsequent to feeding. Weight stabilization was defined as body weight equal to or exceeding that of Day 1 on Day 4 of any 4 day period. Control rats stabilized their weight whereas subjects in all four experimental conditions continued to lose weight and died. More specifically, during final experiment days, experimental animals increased wheel running, lost weight, and in effect, starved themselves to death. There were no significant differences among the four experimental groups which indicates that imposing a "no-activity" interval before or after feeding does not affect self-starvation. This discredits hypotheses which explain self-starvation as a consequence of adventitious reinforcement of wheel running via food presentation.

A second experiment by these researchers investigated feeding duration and self-starvation. Control animals were kept in standard cages, experimental animals in cages with activity wheels. A starvation criterion was defined wherein any rat eating less than 1 g during a feeding period was sacrificed. Results demonstrated that with 1 hour daily food the majority of animals with free wheel access self-starved whereas the majority of animals given 1 hour daily food but no activity wheel stabilized weight. Shorter feeding durations (30 or 45 minutes daily food) did not produce definitive differences between control and experimental animals because all animals tended to starve.

Routtenberg and Kuznesof's third experiment studied novelty stress (stress associated with a new environment) and self-starvation. Results showed that rats allowed several days to adapt to the experimental apparatus before placed on restricted food ate more than non-adapted subjects. Their higher food intake, however, was only for the first several days. Thereafter intake diminished and self-starvation occurred. Thus, reducing novelty stress did not significantly influence self-starvation.

The final experiment investigated depressant drugs and self-starvation. As in the previous studies, control rats were kept in standard cages, experimental rats in cages with activity wheels. When injected with chloropromazine (CPZ), 75% of the experimental subjects stabilized weight and were much less active than those in the previous experiments. Control rats receiving CPZ stabilized weight in a time span typical of other control subjects. These findings imply that CPZ eliminated self-starvation in experimental animals because it suppressed activity. Theoretically, this would disrupt the reciprocal interaction between activity level and food ingestion. An alternative explanation, that CPZ was effective by promoting food intake, is weakened by the finding that control rats stabilized weight in the usual time span. If CPZ increased intake, control animals would have stabilized weight in fewer days than usual.

Adaptation effects and self-starvation were investigated by Routtenberg (1968) who described two stress factors affecting the phenomenon. The first, novelty stress, was previously identified by Routtenberg and Kuznesof (1967). The second factor, deprivation

stress, was considered more critical to self-starvation because unlike novelty stress its suppression of food intake did not subside. Deprivation stress, and ultimately self-starvation, was prevented by either pre-experimental adaptation to restricted food or by CPZ injections. Routtenberg (1968) concluded that deprivation, and thus self-starvation, was a consequence of restricted food in combination with physical activity.

From the research emerge several definitive features of the self-starvation effect. Self-starvation develops in rats and mice given restricted food and free access to an activity wheel. This is verified by the consistent finding that the majority of animals given 1 hour daily food access and 23 hours access to an activity wheel become progressively more active, eat less and suffer severe weight loss.

Also, self-starving animals exhibit extremely high activity levels relative to normal rats (e.g. 10,000 wheels turns/day vs. 500 wheel turns/day). Food intake in self-starving rats is unusually low (e.g. 8 g/day for self-starving rats vs. 14 g/day in control rats or 21 g/day in normal rats).

Self-starvation can be reduced by pre-experimental adaptation to restricted food or by CPZ injections. Adaptation to restricted food is presumed to be effective because it reduces stress associated with deprivation. CPZ is hypothesized to be effective because it suppresses physical activity. A commonality between these treatments is that, theoretically, both disrupt the reciprocal interaction between restricted food and increased physical activity. This reciprocal interaction is critical to the development of self-starvation and is

thus an important premise for a model of self-starvation. Evidence substantiating the influences restricted food and physical activity have upon each other is found in the ethological, operant and human literature.

An example of the effect increased physical activity has upon food intake is provided by Levitsky (1974) who recorded food intake in rats after the introduction of an activity wheel. Results revealed that among those rats who used the wheel, food intake was severely depressed for 4 to 6 days subsequent to the onset of wheel running. Presumably, the increase in physical activity served to depress food intake.

Premack and Premack (1963) postulated that eating and wheel running are equivalent behaviors in the rat's total repertoire of active behaviors. Manipulating the opportunity to engage in one behavior (e.g. wheel running) would thus produce a compensatory increase or decrease in the other behavior (e.g. eating). Their results showed that introduction of an activity wheel produced increased activity concomitant with a voluntary decrease in food ingestion for the first 7 days. Interestingly, these authors also demonstrated that subsequent removal of the activity wheel resulted in increased food intake which persisted even after normal body weight had been restored.

Epstein, Masek and Marshall (1978) investigated methods for improving regulation of food intake in obese children. They found that increasing pre-lunch activity level of the children was associated with decreased caloric intake at the meal. The authors concluded that "since no changes in food preferences were observed, caloric decrease was probably a function of decrease in general food intake" (page 776).

The above studies are consistent in showing that increased physical activity is frequently associated with a voluntary reduction of food intake. The reverse relationship, decreased food availability resulting in increased physical activity, has also been noted in the literature (Cornish and Mrovosky, 1965; Finger, 1951).

For example, Cornish and Mrovosky (1965) investigated activity differences between hibernators and nonhibernators when deprived of food. These authors noted that nonhibernators (rats and guinea pigs) became significantly more active when deprived of food. This finding demonstrates that restricted food is related to activity increases.

Further support is provided by Finger (1951) who showed that activity level is functionally related to food deprivation. Rats deprived of food for 24 hours manifested small increases in wheel running whereas rats deprived for 72 hours exhibited much higher activity levels.

Research thus supports the contention that food intake and physical activity can influence each other. Under conditions of restricted food, increased physical activity is frequently observed. Conversely, increased activity is often associated with voluntary abstention or reduction of food intake. These interactions have been noted in an array of species, including humans, and are central to a model of self-starvation.

In the present study rats on restricted food were randomly assigned to one of five levels of access to an activity wheel. Because opportunity for activity access varied by treatment condition the appropriate measure of activity was rate of wheel running (number of

turns per hour); this allowed intergroup comparisons to be made. Although use of rate as an activity measure was a methodological necessity, it also represents a unique investigative approach to self-starvation. That is, previous studies on self-starvation (Routtenberg and Kuznesof, 1967; Routtenberg, 1968; Epling, Pierce and Stefan, 1981) involved unlimited (i.e. 23 hour) wheel access and so comparisons were made using the total number of wheel turns per day. An hourly rate of wheel running, however, is a finer index of activity which reflects relative intensity of exercise among active animals. Rate of activity may be an important factor in the development and manifestation of self-starvation.

The present study was conducted to investigate the effects of limiting activity for rats placed on a restricted feeding schedule. This restriction may affect activity by reducing net amount of wheel running or by increasing the rate of running. Changes in either rate of running or net number of wheel turns would be expected to affect food ingestion. Thus, the present study will clarify whether amount of activity access differentially affects rate of running and any consequent impact on food ingestion and/or self starvation.

It is further suggested that if rate of running is unaffected across conditions, then as the amount of access to the activity wheel increases:

a) Number of days to stabilization criterion increases for animals stabilizing weight.

b) Number of days to starvation criterion decreases for animals losing weight.

c) The proportion of animals per group meeting stabilization criterion decreases.

d) The proportion of animals per group meeting starvation criterion increases.

e) Food intake decreases.

f) Weight loss increases.

CHAPTER II

METHOD

Subjects

Twenty-four male Sprague-Dawley rats from the university animal colony were approximately 45 days old when the experiment began. None of the animals were littermates.

Apparatus

Apparatae were standard Wahman activity wheels (35 cm diameter) with side cages. The cages included doors which could be used to separate cage and wheel. All wheels had a meter that recorded turns in either direction.

Procedure

A group design was used to investigate food restriction over five levels of wheel access: 23 hour access per day, 12 hour access, 6 hour access, 2 hour access and a control group (no access) (see Table 1). For all conditions food was restricted to a 1 hour daily presentation of Purina Chow pellets. To ensure that starvation was not due to insufficient food, at least 20 g of food was presented at each feeding. Ad lib water was available for all conditions. Although efforts were made to maintain constant light and room conditions, several extreme fluctuations in temperature and humidity occurred.

Table 1
Summary of Independent and Dependent Variables

Independent Variable Daily Activity Wheel Access (5 levels)	Dependent Variables
0 hours (control) 2 hours 6 hours 12 hours 23 hours	Body weight (g per day) Food intake (g per day) Rate of wheel running (wheel turns per hour)

Subjects were randomly assigned to one of the five conditions. On four different occasions animals were inadvertently allowed longer wheel access; these four rats were excluded from the analyses and replaced with new subjects. Four subjects were included in each condition, yielding a total of 20 experimental animals. Because only eight wheels were available it was necessary to conduct the experiment in three phases (in order for 20 subjects to be included). All animals were randomly assigned to an apparatus.

Body weight and number of wheel turns were recorded at the same time each day, just prior to feeding. Food intake was measured via pre/post meal weighing of food pellets. The door between the side cage and the wheel remained open except during food presentation when animals were restricted to the side cage. Wheel access was restricted by tying the wheel so that it was immobile. After feeding, the door to the wheel was opened, the wheels were released, then retied after the appropriate interval (2, 6, 12 or 23 hours). In the control condition the wheel was always tied.

For all conditions, the criterion for removing a subject from the experiment was either:

1. Attainment of 70% of the animal's pre-experimental body weight (Epling et. al. 1981).
2. Weight on Day 4 of any 4 day period greater than or equal to weight on Day 1 of the same period (Routtenberg and Kuznesof, 1967).

CHAPTER III

RESULTS

Prior to statistical analyses, data was processed to equate the number of observations for each subject. This was necessary because of variability among animals of the number of days to starvation or stabilization criterion. The number of observations per subject was inherently determined by the animal(s) meeting starvation or stabilization criterion in the fewest days. Two animals in the 6 hour condition reached starvation criterion in 5 days, therefore five measures of each dependent variable were selected per subject.

Two methods of data analysis were used. The first method used data from the last 5 experimental days. This method was also used by Routtenberg and Kuznesof (1967). A problem with this method is that sampling is restricted to final experimental phases and may thus be nonrepresentative of trends in initial phases of the experiment. This is especially critical in cases where subjects required a relatively long time (e.g. 22 days) to meet criterion.

In view of this drawback, another method of data analysis was also used. First developed by Vincent (1912) and modified by Kjerstad (1919), this technique was used by Epling et. al. (1981). It involves interpolation of data points so that all points are equidistant and encompass the entire range of data. For example, if an animal required 17 days to meet starvation criterion, five interpolated data points correspond to graphical values of the dependent variable at 3.4, 6.8,

10.2, 13.6 and 17.0 days. The distance between each point represents 17/5 days.

Observations selected by both techniques were treated as repeated measures and subjected to analyses of covariance (ANOCOVAR) with trend analysis. Similar analyses were completed on data that excluded observations from inactive animals. These latter analyses were included because of the critical role activity plays in self-starvation; results could be biased by subjects who never engaged in wheel running. Two rats (subject 13 in the 12 hour condition; subject 19 in the 23 hour condition) averaged less than two wheel turns per day and so were excluded from these analyses.

In all ANOCOVARs, the covariate was baseline body weight measured on 3 consecutive pre-experimental days. The variate was one of the three dependent measures (body weight, food intake or rate of wheel running). Also presented in this section is data on time to starvation or stabilization criterion and the proportion of animals stabilizing weight in each condition.

Included in Appendices A - F are results which are either nonsignificant and/or are supplementary to information presented below.

Number of Days to Criterion

Because of the small number of observations per condition for each criterion category (i.e. starvation or stabilization), this data was not amenable to statistical analysis. Qualitative analysis of the data, however, is discussed below.

As can be seen from Table 2, number of days to starvation criterion

do not appear to relate systematically to treatment condition. The 6 hour group met starvation criterion in fewest days followed by the 2 hour, 23 hour, 12 hour and control groups, respectively. These findings discredit the hypothesis that number of days to starvation criterion would increase with less wheel access.

It is of interest to note that subjects in the 6 hour group met starvation criterion in considerably fewer days than did those in other conditions. These animals also showed no variability in the number of days to criterion. These observations suggest that the 6 hour condition was unique in producing rapid weight loss consistent among its subjects.

The number of days to stabilization criterion also do not appear to relate systematically to treatment condition (see Table 3). The 6 hour group stabilized in the fewest days, followed by the 23 hour, control, 2 hour and 12 hour groups, respectively. These findings do not support the hypothesis that as wheel access decreased the number of days to stabilization criterion would decrease.

Number of Animals Reaching Criterion

As is evident in Table 4, there is very limited intergroup variability in the number of animals meeting either starvation or stabilization criterion. A significance test of Chi square reveals no differences ($p > 0.70$) between the number of "starving" vs. "stabilizing" subjects (see Appendix A for this analysis).

Results do not support the hypothesis that the proportion of animals stabilizing their weight would decrease with declining wheel

Table 2

Range and Mean Number of Days to Starvation Criterion

Group	Control	2 hour	6 hour	12 hour	23 hour
Mean	14	9	6	13	11
Range	0	2	5-13	8-22	9-14
n	2	2	3	3	3

Table 3

Range and Mean Number of Days to Stabilization Criterion

Group	Control	2 hour	6 hour	12 hour	23 hour
Mean	14.5	14.5	8	21	12
Range	14-15	14-15	-	-	-
n	2	2	1	1	1

Table 4

Number of Subjects Per Group Reaching Each Criterion

Group	Control	2 hour	6 hour	12 hour	23 hour
CRITERION					
Starvation	2	2	3	3	3
Stabilization	2	2	1	1	1

access. As well, the high proportion of animals meeting starvation criterion in the control group indicates that 1 hour daily food access was not sufficient for animals to stabilize weight.

Pre-Experimental Weight

Pre-experimental body weight was the covariate for ANOCOVARs of experimental weight, food intake and rate of wheel running. Mean pre-experimental weight, based upon 3 days of observations, was lowest for the 6 hour group followed by the 2 hour, 12 hour, control and 23 hour groups, respectively (see Table 5).

Exclusion of non-runners from calculation of mean pre-experimental weight reduced intergroup variability. That is, the 12 hour group mean increased slightly and the 23 hour group mean showed a very large decrease. This latter result suggests that the non-active animal in the 23 hour group was a major source of error variance. It is also of interest to note that the 6 hour group mean was considerably lower than those of the other conditions; the control, 2 hour, 12 hour and 23 hour group means were relatively homogeneous.

Body Weight

ANOCOVARs on body weight violated the statistical model assumption of compound symmetry of covariance matrices. This was indicated by a significant sphericity test ($p = .000$). To ensure that statistics were unbiased, conservative F-tests were conducted (see Appendix B). Results from the conservative F-tests did not alter findings presented below.

Table 5

Mean Pre-experimental Weight (g) for Groups

Group	Control	2 hour	6 hour	12 hour	23 hour
All Animals	256.25	245.75	229.42	248.99	271.58
Non-runners Excluded	256.25	245.75	229.42	252.11	246.22

The ANOCOVAR of Kjerstad data shows that the covariate was highly significant ($F = 87.59$, $df = 1,4$, $p = .000$). The main effect was not significant ($p = .182$). Trend analysis revealed a significant linear trend (($F = 86.56$, $df = 1,15$, $p = .000$) which reflects a within-subjects effect of weight decline over time (adjusted mean weight in g: Time 1 = 221.19, Time 2 = 211.95, Time 3 = 203.79, Time 4 = 195.25, Time 5 = 185.45). A significant interaction for cubic trend by groups also occurred ($F = 3.58$, $df = 4,15$, $p = .030$). Examination of adjusted means suggests that proportion of weight lost over time varies considerably between groups (see Table 6). This observation is clarified by considering percent reduction in body weight for groups over time (see Table 7). It is evident that the 6 hour, 12 hour and 23 hour groups show proportionately greater weight loss from Time 4 to Time 5 than do the control and 2 hour groups. As well, the 23 hour group manifests a much higher weight reduction than the 12 hour and 6 hour groups. The control and 2 hour groups show a tendency to decrease rate of weight loss over time. These observations suggest intense weight loss during final experimental days for the 6 hour, 12 hour and particularly, the 23 hour group. This tendency contrasts with the control and 2 hour groups which tend to minimize weight loss during final experimental days.

Equivalent ANOCOVARs were completed on the other three sets of data (Kjerstad data with non-runners excluded; last 5 days data; last 5 days data with non-runners excluded). Results were highly consistent with those above (see Appendices C and D). An exception was noted in that

Table 6

Adjusted Mean Weight (g) for Groups Over Time

Group	Control	2 hour	6 hour	12 hour	23 hour
Time 1	222.60	219.49	221.26	214.30	228.34
Time 2	215.10	208.74	213.51	203.30	214.09
Time 3	206.60	200.74	205.76	195.80	210.09
Time 4	198.60	192.24	197.01	187.30	201.09
Time 5	196.10	187.24	184.51	176.80	182.59

Table 7

Percent Reduction in Weight for Groups Between Time Points

Group	Control	2 hour	6 hour	12 hour	23 hour
Time					
1 to 2	3.40	4.80	3.50	5.10	6.20
2 to 3	3.90	3.80	3.60	3.70	1.87
3 to 4	3.80	4.20	4.20	4.30	4.20
4 to 5	1.25	2.60	6.30	5.60	9.20

a significant cubic trend by group interaction did not occur in the last 5 days data.[1]

Results from analyses of weight show that although the main effect was not significant and all groups showed a trend of weight loss over time, the rate of weight loss for groups varied between time points. The 6 hour, 12 hour and 23 hour groups manifested a high proportion of weight loss near the end of the experiment. This was most marked in the 23 hour group. The control and 2 hour groups decreased their rate of weight loss over time.

Food Intake

The ANOVOCAR of Kjerstad data revealed a highly significant covariate ($F = 18.08$, $df = 1,14$, $p = .000$). The main effect was nonsignificant ($p = .084$). Trend analysis revealed a significant quadratic trend ($F = 14.28$, $df = 1,15$, $p = .002$); this is consistent with the within-subjects effect of increasing food intake from Time 1 to Time 3 with subsequent decreases from Time 3 to Time 5 (adjusted mean intake in g: Time 1 = 8.19, Time 2 = 9.56, Time 3 = 9.86, Time 4 = 9.61, Time 5 = 8.73).

ANOVOCAR of Kjerstad data with non-runners excluded produced highly similar results (see Appendices C and D). An exception is a significant quadratic trend by group interaction ($F = 6.75$, $df = 4.13$, $p = .039$). Graphical representation of the means (see Figure 1) depicts

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[1] This discrepancy reflects the fact that the Kjerstad data and the last 5 days data sample observations from different stages of the experiment.

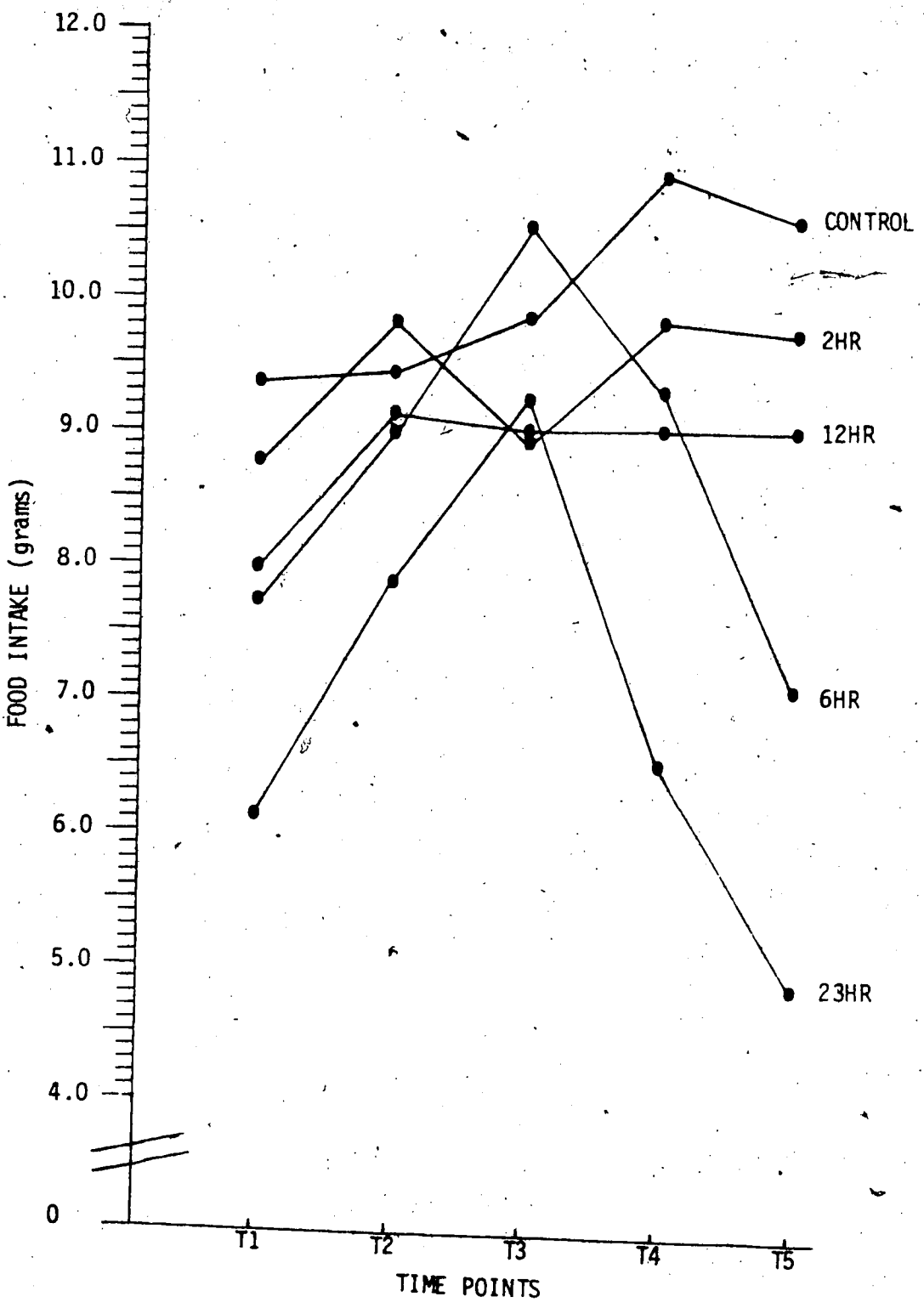

Figure 1

Adjusted Mean Food Intake Over Time For Groups

a quadratic trend for the 6 hour and 23 hour conditions. It is noted that this trend of food intake characterizes self-starving rats (e.g. Routtenberg and Kuznesof, 1967; Routtenberg, 1968; Epling et. al., 1981). Also evident in Figure 1 is the tendency of the control, 2 hour and 12 hour groups to increase, then stabilize, food intake. Among these three groups, the control group maintained the highest intake level, followed by the 2 hour and 12 hour groups, respectively.

Results from the ANOCOVAR of the last 5 days data differ from Kjerstad data analyses (see Appendices C and D). The covariate was highly significant ($F = 19.24$, $df = 1,14$, $p = .000$). The main effect was very nearly significant ($p = .0505$). Examination of adjusted mean intake for each group reveals that over the last 5 experimental days, the control group had the highest intake followed by the 2 hour, 6 hour, 12 hour, and 23 hour groups, respectively (see Table 8). Trend analysis did not yield any significant results for quadratic or linear trends.[2]

Exclusion of non-runners from the above analysis altered findings in that the main effect was more highly significant ($F = 3.40$, $df = 4,12$, $p = .044$). A significant linear trend occurred ($F = 16.88$, $df = 1,13$, $p = .043$) which reflects a within-subjects effect of increased intake from Time 2 to Time 4 (see Table 9). Consideration of ingestion patterns depicted in Figure 1 suggests that the linear trend is generally attributable to the control, 2 hour and 12 hour groups

---

2 A significant cubic trend occurred but a meaningful interpretation was limited by the complexity of such a trend.

Table 8

Adjusted Mean Food Intake (g) for Groups

Group	Control	2 hour	6 hour	12 hour	23 hour
	10.87	10.54	9.51	9.29	7.34

Table 9

Adjusted Mean Food Intake (g) for Subjects Over Time

Time	1	2	3	4	5
	10.08	9.54	9.56	9.88	8.59

which manifest small increases of intake over the course of the experiment. However, the decrease of intake from Time 4 to Time 5 which is evident in Table 9, reflects the 6 hour and 23 hour groups' tendency to decrease intake during their final experimental days (also see Figure 1).

To summarize, analyses of food intake reveal that during the last 5 experimental days amount of wheel access significantly influenced food intake. That is, the control group had the highest intake, followed by the 2 hour, 6 hour, 12 hour and 23 hour groups, respectively. The hypothesis that food intake would decrease with increased wheel access is supported by these results. Trend analysis revealed significantly different patterns of intake between groups over time. The 6 hour and 23 hour groups showed a pattern of ingestion which characterizes self-starvation - initial increases of intake with subsequent decreases during final experimental days. The control group increased intake over the experiment whereas the 2 hour and 12 hour groups initially increased food intake and then tended to maintain it.

Rate of Wheel Running[3]

As with analyses of body weight, ANOCOVARs of rate of running violated statistical model assumptions. With one exception conservative F-tests did not alter the findings presented below. (See Appendix D for these conservative F-tests).

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3 Analysis on rate of wheel running included only the four experimental conditions since control animals did not have wheel access.

The ANOCOVAR of Kjerstad data revealed a significant covariate ($F = 4.87$, $df = 1,11$, $p = .049$). The main effect was non-significant ($p = .387$). Trend analysis showed significant linear ($F = 24.69$, $df = 1,12$, $p = .000$) and quadratic ($F = 20.65$, $df = 1,12$, $p = .000$) trends. These trends are consistent with a within-subjects effect of rate increases over time, most marked from Time 4 to Time 5 (adjusted mean number of wheel turns per hour: Time 1 = 29.37, Time 2 = 37.81, Time 3 = 65.37, Time 4 = 166.68, Time 5 = 345.23). Exclusion of non-runners from a subsequent ANOCOVAR did not alter these results (see Appendices C and D).

ANOCOVARs of the last 5 days data produced findings similar to those above (see Appendices C and D). An exception is a significant quadratic trend by group interaction ($F = 4.86$, $df = 3,12$, $p = .019$), found in the last 5 days data, all animals included.[4] Examination of adjusted means shows large rate increases for all groups from Time 3 to Time 4 and from Time 4 to Time 5 (see Table 10). It is also noted that at Time 5, the 6 hour group displayed the highest rate of running, followed by the 23 hour, 12 hour and 2 hour groups, respectively.

These findings on rate of wheel running must also be considered in light of the net number of wheel turns for the last 5 days data, all animals included (see Table 11). When number of wheel turns is considered, the 23 hour group displays the highest number followed by the 6 hour, 12 hour and 2 hour groups, respectively.

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[4] By use of the conservative F-test, this result became NS at = .05.

Table 10

Adjusted Mean Rate (turns/hour) for Groups Over Time

Group	2 hour	6 hour	12 hour	23 hour
Time 1	31.22	-8.06	26.64	80.71
Time 2	47.22	5.94	54.39	117.46
Time 3	84.72	27.94	120.39	254.46
Time 4	109.97	231.44	188.64	272.46
Time 5	173.72	555.44	272.89	376.46

Table 11

Adjusted Mean Number of Wheel Turns for Groups Over Time[5]

Group	2 hour	6 hour	12 hour	23 hour
Time 1	62.44	-48.36	319.68	1856.33
Time 2	94.44	35.64	652.68	2701.58
Time 3	169.44	167.64	1444.68	5852.58
Time 4	219.94	1388.64	2263.68	6266.58
Time 5	347.44	3332.64	3274.68	8658.58

[5] Mean number of wheel turns were calculated from mean rates presented in Table 10.

Results show that rate of wheel running tended to increase with increased wheel access but this trend was disrupted by the 6 hour condition. This group displayed the highest rate followed by the 23 hour, 12 hour and 2 hour groups, respectively. The 2 hour group differed from the 6 hour, 12 hour and 23 hour groups in its relatively low net amount and rate of wheel running; this was most apparent at Time 5.

All groups displayed increases in rate of running over time. These increases were most marked from Time 4 to Time 5.

Summary of Results

Number of days to starvation or stabilization criterion did not systematically relate to treatment condition. Of interest was the 6 hour group's rapid progression to criterion which may reflect its low pre-experimental weight.

The proportion of animals meeting stabilization criterion did not differ significantly from the proportion meeting starvation criterion. This result, as well as lack of intergroup differences for the proportion of rats reaching starvation criterion and especially the high proportion of control subjects reaching starvation criterion, suggests the 1 hour feeding procedure was too severe.

Analyses on experimental weight indicated no significant main effects. However, a significant interaction revealed that the 6 hour, 12 hour and especially the 23 hour group lost weight very rapidly during the final experimental days. This contrasts with the control and 2 hour groups which, over the same time span, slowed weight loss.

Over the last 5 experimental days, food intake was inversely related to amount of wheel access. The 23 hour group had the lowest mean intake, followed by the 12 hour, 6 hour, 2 hour and control groups, respectively. The 6 hour and 12 hour groups were very close to each other in their mean intake, as were the control and 2 hour groups. Trend analysis revealed that over the course of the experiment, the control group tended to increase intake and the 2 hour and 12 hour groups maintained intake. The 6 hour and 23 hour groups showed initial increases and subsequent decreases in food intake and thus were the only groups manifesting an ingestion pattern typical of self-starvation.

Rate of wheel running did not increase as amount of wheel access decreased. The 6 hour group was unique in its very high rate of running; the 23 hour group had the next highest rate, followed by the 12 hour and 2 hour groups, respectively. Net amount of activity tended to increase with increasing wheel access, an exception being the 6 hour group. That is, the 23 hour group had the highest number of wheel turns followed by the 6 hour, 12 hour and 2 hour groups, respectively. By either measure of activity (rate of running or net number of wheel turns) the 6 hour and 23 hour groups were most active, followed by the 12 hour group, and then the 2 hour group. These findings indicate that different amounts of access to an activity wheel were associated with different rates and net amounts of wheel running; neither rate of running or net number of wheel turns increased directly with increases in the amount of wheel access.

Integration of the above results indicates that only the 6 hour and 23 hour groups manifested trends typifying self-starvation - declining food ingestion concomitant with rapid weight loss and an extremely high activity level.

CHAPTER IV

DISCUSSION

Inferences from results of the present study are limited by the high proportion of rats in the control and 2 hour groups that met starvation criterion. This unexpected finding reflects two interrelated factors and their consideration is necessary to clarify the effects of limiting activity access on self-starvation. First, a 1 hour daily food ration may be inadequate for weight stabilization. This was exemplified by two control animals who, despite no wheel access, reached 70% body weight. Routtenberg and Kuznesof (1967) reported that one of five rats given 1 hour daily food and no wheel access failed to stabilize weight. Their data, as well as findings from the present study, indicate that 1 hour daily food may be insufficient to maintain body weight since a significant proportion of control rats on this food schedule are unable to stabilize weight.

Secondly, the high proportion of starving animals in the present study may be attributed to the 70% pre-experimental weight criterion. This criterion implies that the majority of animals in the present study self-starved although significant intergroup differences occurred for weight loss, food intake and wheel running. For example, the 2 hour group decreased weight loss over time, maintained relatively high food ingestion and showed little wheel running; this contrasts with the 6 hour group which increased weight loss over time, decreased intake

and showed a very high rate and net amount of wheel running. These marked differences between the two conditions, however, are obscured since application of the 70% criterion classifies a large proportion of rats in each group as meeting starvation criterion.

An alternative criterion of starvation is provided by Routtenberg and Kuznesof (1967) who defined manifestation of self-starvation as food intake less than 1 g on any experimental day. Because the self-starvation model is based upon a reciprocal interaction between increased activity and decreasing food ingestion, Routtenberg and Kuznesof's (1967) criterion of starvation may be more appropriate since it directly reflects food ingestion. Seventy per cent pre-experimental weight however, is only an indirect indicator of intake.

Application of Routtenberg and Kuznesof's (1967) self-starvation criterion to the present study clarifies treatment effects. Examination of ingestion patterns (see Fig. 1) suggests that if the present study had been extended for several days the 6 hour and 23 hour groups would likely have met the starvation criterion of food intake less than 1 g. Trends of the control, 2 hour and 12 hour groups, however, imply that intake would likely have been maintained at a fairly high level, counterindicating self-starvation.

Number of days to stabilization or starvation criterion (70% weight) did not systematically relate to treatment condition. It was predicted that if limiting wheel access suppressed running, then as access to activity decreased, the number of days to stabilization or starvation criteria would also decrease. Whereas results did not support these hypotheses, the rapid progression of the 6 hour group to

weight was of interest. The 6 hour group was also unique in its relatively low pre-experimental weight which suggests that lower baseline weight may contribute to rapid, severe weight loss.

No intergroup differences were found for net weight loss although distinct trends occurred among groups. Rats in the 6 hour, 12 hour and 23 hour groups lost weight very quickly during final experimental days whereas the control and 2 hour groups slowed weight loss.

Food intake for the last five experimental days was inversely related to amount of wheel access. This supports the prediction that intake would increase as wheel access decreased. However, different patterns of ingestion were evident. The control group tended to increase intake over time and the 2 hour and 12 hour groups maintained intake. The 6 hour and 23 hour groups showed intake patterns typical of self-starving animals - initial increases and subsequent decreases.

The hypothesis concerning net number of wheel turns was not fully supported. Decreased wheel access was generally associated with decreased net activity. The 6 hour group, however, exceeded the 12 hour group's net activity.

Rate of wheel running did not increase as wheel access increased. All groups showed increases in rate over time. These increases were most marked during the last 2 experimental days, especially for the 6 hour, 12 hour and 23 hour conditions. Over the final experimental days, the 6 hour group had the highest rate of wheel running, followed by the 23 hour, 12 hour and 2 hour groups, respectively.

It is noted that the relatively high rate of running of the 6 hour and 23 hour groups coincides with rapid weight loss and declining food intake. These features clearly suggest self-starvation and thus imply that the effect can develop with alternate activity levels. Both a moderate rate of running for prolonged duration (23 hour condition) and a high rate of running for relatively short duration (6 hour condition) were associated with classic manifestation of self-starvation. That different activity levels were shown in the two groups is of interest and can be explained by considering that either high rate activity for brief periods or moderate rate activity for prolonged periods exert the same suppressing effect on food intake. Studies by Mayer et.al. (1954) and Martin et.al. (1979) demonstrate that depending upon rate or duration, activity level can differentially influence food ingestion.

Mayer et.al. (1954) exercised female rats on a treadmill for increasing time spans each day. At moderate durations (20 to 60 minutes) a significant decrease of intake occurred. For longer durations (2 hours), intake was maintained at pre-experimental levels. Prolonged durations (6 hours) resulted in a linear increase of intake and no weight change.

Similarly, Katch, Martin and Martin (1979) used two levels of exercise (high vs. low) to assess its effect on food consumption in male rats. Exercise levels were equated for caloric expenditure but the high intensity group was required to complete its exercise in less time (50 minutes) than the low intensity group (60 minutes). A non-exercised control group was also included. Results showed that the exercised group ate significantly less than the non-exercised one.

Among exercised subjects, the high intensity group gained weight less rapidly. Katch et.al. concluded that "it is not necessarily total energy expenditure which affects food consumption. Rather, some factors related to the degree of effort (intensity) may be the key factor influencing food consumption following exercise." (p. 1406).

The influential variable in Katch et.al's (1979) study was not net caloric expenditure or duration of exercise but a combination of the two - rate of caloric expenditure. When this is considered, the "degree of effort" to which the authors refer is very likely rate of caloric expenditure, which was greater for the high intensity group.

Although the above studies differed from the present one in several ways (eg. food availability; duration of activity; enforced activity), they are important because they demonstrate that varying amounts of exercise produced variations in food consumption. This may also account for food intake patterns in the present study. The 6 hour and 23 hour groups may have shown declining food intake because of their intense exercise. As well, the less intense activity of the 2 hour and 12 hour conditions may have promoted higher intake.

Results from the present study have several implications for a model of self-starvation. First, given restricted food, self-starvation can occur with 6 or 23 hours of daily wheel access. Second, different amounts of activity access result in varying intensities of exercise. Six hour access resulted in a high rate of running (number of wheel turns per hour), 23 hours produced a very high net amount of running (total number of wheel turns per day), 12 hours a moderate rate and amount of activity and 2 hours resulted in low

activity. Third, activity level may exert differential influences on food intake. Very intense running (6 and 23 hour groups) was linked with declining intake, less intense running with maintenance of ingestion (2 and 12 hour groups).

These findings may also have implications for anorexia nervosa and obesity in humans. The rationale for applying the self-starvation model to these disorders is that, like self-starvation, anorexia nervosa and obesity have both been associated with deviations in food intake and/or activity level. Decreased eating and hyperactivity have been suggested as contributing factors in anorexia nervosa (e.g. Smith, 1980; Kron et.al. 1978). Lack of exercise has been cited as a precipitating factor in obesity (e.g. Bloom and Eidex, 1967; Thompson et.al. 1982). Thus, aberrant patterns of food intake and activity level are common to anorexia nervosa and obesity in humans and to self-starvation in rats. These commonalities imply that findings from the present study may be usefully applied to human weight disorders. Extension of findings from the present study to anorexia nervosa and obesity is discussed below.

Implications and Extension to Human Weight Disorders

Like self-starvation, a primary feature of anorexia nervosa is the subject's decreased food intake. This decrease is of such severity that debilitating weight loss, and often death, ensues. Hyperactivity as an exacerbating variable in anorexia nervosa has not been systematically researched, although it has been noted in clinical studies. That is, very high activity levels in conjunction with reduced food intake and severe weight loss have been reported.

For example, Smith (1980) noted the increasing incidence of severe, detrimental weight loss among young male athletes, in a manner analogous to anorexia nervosa. He attributed the weight loss to prolonged voluntary reduction of food intake while adhering to a rigorous physical training program.

An investigation of hyperactivity and anorexia nervosa was undertaken by Kron et.al. (1980). Hyperactivity was operationally defined as an exercise level greater than that of peers and including strenuous activity (e.g. swimming, jogging). Activity levels were reviewed for 33 women hospitalized for anorexia nervosa. Of the 33 women, 21 were premorbidly hyperactive and 25 of these women were also hyperactive when hospitalized. In a follow-up study of 15 of the women, 11 continued to be hyperactive; all of these 11 women had been premorbidly hyperactive. Kron et.al. (1978) concluded that "hyperactivity is an early and enduring feature of anorexia nervosa ..." (p. 439).

Evidence thus suggests that hyperactivity and reduced food intake are central features of anorexia nervosa and the self-starvation effect. A striking contrast to these disorders is obesity, which has typically been associated with inactivity (e.g. Bloom and Eidex, 1967; Thompson et.al., 1982). For example, activity levels in obese and lean humans were studied by Bloom and Eidex (1967). They reported that obese subjects were significantly less active than lean subjects as measured by daily indices such as time spent on their feet and time per day spent in bed.

A study by Mavissakalian (1982) provides an interesting link between anorexia nervosa and obesity. He found that preventing exercise for 1 hour after meals facilitated weight gain in two female patients hospitalized with anorexia nervosa. Continuation of this therapy program after release from hospital resulted in both women becoming obese. According to the self-starvation model, postmeal prevention of exercise facilitated weight gain because the suppression of food intake by activity was disrupted.

Consideration of findings from the present study for the development and treatment of anorexia nervosa explicates the need to monitor intensity of exercise in anorexic patients; hyperactivity associated with the disorder may be attributed specifically to intense exercise (i.e. of high rate and/or prolonged duration). Treatment of anorexia nervosa through behavior modification techniques could incorporate a contingency between food consumption and activity wherein the activity was controlled for intensity (rate and duration). A similar approach would also be useful as a post-treatment means to help ensure weight gain is maintained.

Treatment of obesity may be advanced by implementing exercise programs requiring a high rate of energy expenditure over moderate time spans or lower rate exercise for prolonged durations. The benefits of this may be twofold - increased metabolic requirements and, according to findings from the present study, declining food intake. Both effects, of course, would theoretically promote weight loss.

Findings from the present study are important in demonstrating that due to changes in rate of running, limiting wheel access does not have a direct effect of limiting activity in rats on restricted food. Furthermore, rate of wheel running is an influential variable in the self-starvation effect. That is, a very high rate of running, as shown by rats allowed 6 hours of wheel access per day, appears to exert the same suppressing effect on food intake as a moderate rate of running for prolonged duration (23 hour condition). Because of possible confounding effects of inadequate daily food presentation and an inappropriate starvation criterion, however, a critical precedent for future research is replication of the present study but with modifications to clarify treatment effects for no, 2 hour or 12 hours of wheel access. Such modifications should include extension of daily food access (e.g. to 90 minutes) as well as a starvation criterion based on daily food intake.

With regard to the latter modification, it is suggested that Routtenberg and Kuznesof's (1967) criterion of 1 g of food on any day may be too stringent and could present ethical problems. Use of a higher criterion (e.g. 5 g per day), however, would likely circumvent this potential complication and still be effective in indicating declining food intake. If daily food intake is employed as a starvation criterion, it may also be useful to implement an equivalent definition for weight stabilization. An example is stabilization defined as food intake on Day 4 of any 4 day period equal to or exceeding that on Day 1. Use of such a criterion would provide

methodological consistency and also allow sensitivity to increases in food intake which counterindicate self-starvation.

Experimental manipulation of rate of wheel running in future research will likely provide a practical method for investigating the role of intensity of exercise in self-starvation in rats. It is feasible that such research will also provide the impetus and direction for investigating intensity of exercise and human weight disorders, specifically anorexia nervosa and obesity.

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APPENDIX A

TEST OF CHI SQUARE - "STARVING" vs. "STABILIZING" SUBJECTS

Table A

Frequencies of Stabilizing vs. Starving Subjects

Criterion	Starvation		Stabilization	
	Observed Frequency	Expected Frequency	Observed Frequency	Expected Frequency
Group				
Control	2	2.6	2	1.4
2HR	2	2.6	2	1.4
6HR	3	2.6	1	1.4
12HR	3	2.6	1	1.4
23HR	3	2.6	1	1.4
Total	13		7	

n = 4

df = 4

Obtained Chi Square = 1.747

P(Chi Square $\geq$ 1.747) $>$ 0.70

APPENDIX B

CONSERVATIVE F-TESTS

Table A

Conservative F-tests

Dependent Variable	Data Pool	Source	Obtained F	d.f.	Greenhouse Geisser Coefficient	Corrected d.f.	Conservative F
1. WEIGHT	Kjerstad	Weight over Time	65.51	4,60	0.339	1,20	4.35
		Group X Time	0.65	16,60	0.339	5,20	2.71
	Kjerstad Nonrunners excluded	Weight over Time	78.15	4,52	0.337	1,18	4.41
		Group X Time	1.34	16,52	0.337	5,18	2.77
	Last 5 Days	Weight over Time	20.22	4,60	0.278	1,17	4.45
		Group X Time	1.36	16,60	0.278	4,17	2.96
	Last 5 Days Nonrunners excluded	Weight over Time	28.16	4,52	0.285	1,15	4.54
		Group X Time	2.18	16,52	0.285	5,15	2.90
2. RATE	Kjerstad	Weight over Time	22.02	4,48	0.322	1,15	4.54
		Group X Time	2.29	12,48	0.322	4,15	3.06
	Kjerstad Nonrunners excluded	Weight over Time	20.26	4,40	0.303	1,12	4.75
		Group X Time	2.07	12,40	0.303	4,12	3.26
	Last 5 days	Weight over Time	21.49	4,48	0.378	2,18	3.55
		Group X Time	2.44	12,48	0.378	4,18	2.93
	Last 5 days Nonrunners excluded	Weight over Time	26.02	4,40	0.387	2,16	3.63
		Group X Time	2.54	12,40	0.387	5,16	2.85

APPENDIX C

ADJUSTED MEANS FOR DEPENDENT MEASURES

ADJUSTED MEANS FOR WEIGHT (grams)

Table A
Kjerstad Data, Non-runners Excluded

Group		Control	2HR	6HR	12HR	23HR
Time	1	220.62	217.07	218.16	213.89	226.97
	2	213.12	206.32	210.41	203.56	212.64
	3	204.62	198.32	202.66	195.89	209.64
	4	196.62	189.82	193.91	184.89	198.64
	5	194.12	184.82	181.41	171.55	179.29

Table B
Last 5 Days Data

Group		Control	2HR	6HR	12HR	23HR
Time	1	203.08	198.62	213.83	193.44	210.54
	2	199.32	196.62	208.83	191.44	208.54
	3	198.32	193.37	201.33	188.44	200.29
	4	196.58	190.37	193.58	183.19	192.54
	5	196.58	186.87	182.83	177.19	184.04

Table C
Last 5 Days Data, Non-runners Excluded

Group		Control	2HR	6HR	12HR	23HR
Time	1	202.02	196.34	209.64	193.98	209.37
	2	198.27	194.34	204.64	191.98	207.37
	3	197.27	191.09	197.14	187.31	196.37
	4	195.52	188.09	189.39	180.98	186.69
	5	195.52	184.57	178.64	172.31	174.03

ADJUSTED MEANS FOR FOOD INTAKE (grams)

Table D
Kjerstad Data, Non-runners Excluded

Group	Control	2HR	6HR	12HR	23HR
Time 1	9.37	8.78	7.76	7.99	6.29
2	9.47	9.86	9.08	9.12	7.89
3	9.89	8.91	10.54	8.92	9.26
4	10.97	9.88	9.36	8.96	6.53
5	10.59	9.76	7.14	8.96	4.83

Table E
Last 5 Days Data

Group	Control	2HR	6HR	12HR	23HR
Time 1	10.57	11.74	9.53	9.68	8.88
2	11.07	9.86	10.47	9.38	6.93
3	10.62	10.78	10.18	8.98	7.23
4	11.42	10.41	9.73	9.58	7.81
5	10.67	9.94	7.65	8.85	5.86

Table F
Last 5 Days Data, Non-runners Excluded

Group	Control	2HR	6HR	12HR	23HR
Time 1	10.47	11.49	9.06	8.88	9.30
2	10.97	9.61	10.01	8.88	6.53
3	10.52	10.54	10.54	8.88	6.67
4	11.32	10.16	10.16	9.11	6.70
5	10.57	9.69	9.69	8.94	4.80

ADJUSTED MEANS FOR RATE OF WHEEL RUNNING (turns/hour)

Table G
Kjerstad Data, Non-runners Excluded

Group	2HR	6HR	12HR	23HR
Time 1	54.24	-2.93	25.59	57.23
2	63.99	-2.68	42.59	62.32
3	103.49	17.57	71.59	84.32
4	101.74	210.32	144.59	191.32
5	177.49	562.82	369.93	350.65

Table H
Last 5 Days Data

Group	2HR	6HR	12HR	23HR
Time 1	31.22	-8.06	26.64	80.71
2	47.22	5.94	54.39	117.46
3	84.72	27.94	120.39	254.46
4	109.97	231.44	188.64	272.46
5	173.72	555.44	272.89	376.46

Table I
Last 5 Days Data, Non-runners Excluded

Group	2HR	6HR	12HR	23HR
Time 1	40.09	8.39	47.93	60.76
2	56.09	22.39	84.59	109.42
3	93.59	44.39	172.93	292.42
4	118.84	247.89	263.59	316.42
5	182.59	571.89	376.26	454.75

APPENDIX D

ANOCOVARS OF DEPENDENT MEASURES

ANOCOVARS OF WEIGHT

Table A
Kjerstad Data

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	1935.905	4	483.976	1.81	.182
1-st Covar	23383.855	1	23383.855	87.59	.000
Error	3737.394	14	266.956		
M(1)	15207.680	1	15207.680	86.56	.000
M(1)G	269.320	4	67.330	.38	
Error	2635.200	15	175.680		
M(2)	.357	1	.357	.01	.929
M(2)G	149.285	4	37.324	.85	.518
Error	662.214	15	44.147		
M(3)	37.845	1	37.845	3.54	.079
M(3)G	153.030	4	38.257	3.58	.030
Error	160.425	15	10.695		

Table B
Kjerstad Data, Non-runners Excluded

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	1405.908	4	351.477	1.17	.371
1-st Covar	13449.100	1	13449.100	44.84	.000
Error	3599.182	12	299.931		
M(1)	15317.696	1	15317.696	95.50	.000
M(1)G	550.233	4	139.808	.87	.506
Error	2085.166	13	160.397		
M(2)	42.403	1	42.403	1.65	.221
M(2)G	294.841	4	73.710	2.86	.066
Error	334.952	13	25.765		
M(3)	53.382	1	53.382	6.13	.027
M(3)G	198.377	4	49.594	5.69	.007
Error	113.250	13	8.711		

Table C
Last 5 Days Data

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	1624.544	4	406.136	0.80	.549
1-st Covar	8200.164	1	8200.164	16.11	.001
Error	6107.118	12	508.926		
M(1)	5085.706	1	5085.706	30.84	.000
M(1)G	1444.086	4	361.021	2.19	.127
Error	2143.958	13	164.919		
M(2)	92.146	1	92.146	7.61	.016
M(2)G	115.156	4	28.789	2.38	.105
Error	157.446	13	12.111		
M(3)	2.200	1	2.200	.66	.429
M(3)G	10.136	4	2.534	.77	.566
Error	43.041	13	3.310		

Table D
Last 5 Days Data, Non-runners Excluded

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	2544.562	4	636.140	1.25	.336
1-st Covar	18654.775	1	18654.775	36.53	.000
Error	7149.574	14	510.683		
M(1)	4324.500	1	4324.500	21.89	.000
M(1)G	1084.400	4	271.100	1.37	.290
Error	2963.900	15	197.593		
M(2)	53.175	1	53.157	3.54	.079
M(2)G	76.128	4	19.032	1.27	.325
Error	225.000	15	15.000		
M(3)	2.000	1	2.000	.69	.418
M(3)G	10.850	4	2.712	.94	.468
Error	43.350	15	2.890		

ANOCOVARS OF FOOD INTAKE

Table E
Kjerstad Data

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	8765.109	4	2191.277	2.56	.084
1-st Covar	15457.083	1	15457.083	18.08	.000
Error	11966.966	14	854.783		
M(1)	330.245	1	330.245	.98	.338
M(1)G	759.230	4	189.807	.56	.694
Error	5073.825	15	338.255		
M(2)	3202.889	1	3202.889	14.28	.001
M(2)G	2255.235	4	563.808	2.51	.085
Error	3364.517	15	224.301		
M(3)	2.205	1	2.205	.02	.889
M(3)G	348.320	4	87.080	.78	.552
Error	1664.175	15	110.945		

Table F
Kjerstad Data, Non-runners Excluded

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	89.518	4	22.379	2.70	.081
1-st Covar	85.584	1	85.584	10.33	.007
Error	99.386	12	8.382		
M(1)	.412	1	.412	.15	.708
M(1)G	13.837	4	3.459	1.22	.348
Error	36.751	13	2.827		
M(2)	27.216	1	27.216	13.88	.002
M(2)G	27.007	4	6.751	3.44	.039
Error	25.482	13	1.960		
M(3)	.020	1	.020	.02	.900
M(3)G	3.142	4	.785	.62	.657
Error	16.519	13	1.270		

Table G
Last 5 Days Data

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	14172.212	4	3543.053	3.10	.050
1-st Covar	21976.008	1	21976.008	19.24	.000
Error	15994.691	14	1142.477		
M(1)	1485.125	1	1485.125	3.48	.081
M(1)G	864.400	4	216.100	.51	.731
Error	6397.175	15	426.478		
M(2)	174.432	1	174.432	1.22	.286
M(2)G	1035.585	4	258.896	1.81	.179
Error	2143.339	15	143.889		
M(3)	780.125	1	780.125	6.68	.020
M(3)G	548.350	4	137.087	1.17	.361
Error	1751.825	15	116.788		

Table H
Last 5 Days Data, Non-runners Excluded

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	160.074	4	40.018	3.40	.044
1-st Covar	94.030	1	94.030	7.99	.015
Error	141.199	12	11.766		
M(1)	16.885	1	16.885	4.99	.043
M(1)G	19.548	4	4.887	1.45	.274
Error	43.951	13	3.380		
M(2)	.896	1	.896	0.59	.457
M(2)G	11.273	4	2.818	1.85	.180
Error	19.849	13	1.526		
M(3)	5.856	1	5.856	4.56	.052
M(3)G	5.212	4	1.303	1.01	.435
Error	16.697	13	1.284		

ANOCOVARS OF RATE OF WHEEL RUNNING

Table I
Kjerstad Data

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	82259.600	3	27419.866	1.10	.388
1-st Covar	120950.007	1	120950.007	4.87	.049
Error	273209.042	11	24837.268		
M(1)	925376.400	1	925376.400	24.69	.000
M(1)G	239753.150	3	79917.716	2.13	.149
Error	449723.850	12	37476.987		
M(2)	195762.875	1	195762.875	20.65	.000
M(2)G	92912.803	3	31304.267	3.30	.057
Error	113751.035	12	9479.252		
M(3)	5394.006	1	5394.006	2.43	.144
M(3)G	9325.068	3	3108.356	1.40	.290
Error	26612.025	12	2217.668		

Table J
Kjerstad Data, Non-runners Excluded

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	37108.479	3	12339.493	0.63	.613
1-st Covar	131570.770	1	131570.770	6.72	.029
Error	176154.912	9	19572.768		
M(1)	842464.072	1	842464.072	20.33	.001
M(1)G	226953.263	3	75651.421	1.94	.187
Error	389893.308	10	38989.330		
M(2)	203264.551	1	203264.551	20.33	.001
M(2)G	89581.238	3	29860.412		
Error	99977.148	10	9997.714		
M(3)	11304.859	1	11304.859	8.07	.017
M(3)G	3358.552	3	1119.517	.80	.522
Error	14003.483	10	1400.348		

Table K
Last 5 Days Data

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	164854.795	3	54951.598	1.43	.286
1-st Covar	189573.927	1	189573.927	4.93	.048
Error	422717.572	11	38428.870		
M(1)	944640.225	1	944640.225	28.23	.000
M(1)G	215465.425	3	71821.808	2.15	.147
Error	401527.550	12	33460.629		
M(2)	73660.017	1	73660.017	9.28	.010
M(2)G	115727 303	3	38575.767	4.86	.019
Error	95245.535	12	7937.127		
M(3)	864.900	1	864.900	.25	.626
M(3)G	4592.450	3	1530.816	.44	.728
Error	41682.450	12	3473.537		

Table L
Last 5 Days Data, Non-runners Excluded

Source	Sum of Squares	Degrees of Freedom	Mean Square	F	Prob.
Group	194031.760	3	64677.253	2.49	.126
1-st Covar	73482.102	1	73482.102	2.83	.127
Error	234021.364	9	26002.373		
M(1)	1068631.929	1	1068631.929	38.85	.000
M(1)G	207170.451	3	69056.817	2.51	.118
Error	275049.441	10	27504.944		
M(2)	68716.143	1	68716.143	7.32	.022
M(2)G	106491.928	3	35497.316	3.78	.047
Error	93916.220	10	9391.622		
M(3)	546.288	1	546.288	.13	.724
M(3)G	4589.554	3	1529.851	.37	.777
Error	41576.766	10	4157.676		

APPENDIX-E

ANOVAS OF DEPENDENT MEASURES

ANALYSES OF VARIANCE - KJERSTAD DATA, ALL ANIMALS INCLUDED

Anova of Body Weight

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	15843.750	4	3960.938	2.191	.119
S-Within	27116.000	15	1807.733		
B	15252.000	4	3813.000	65.384	.001
AB	576.750	16	36.047	.618	.857
BS-Within	3499.000	60	58.317		

Anova of Food

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	86.190	4	21.548	1.173	.362
S-Within	275.531	15	18.369		
B	34.690	4	8.673	4.596	.003
AB	42.067	16	2.629	1.393	.176
BS-Within	113.230	60	1.887		

Anova of Wheel Running

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	68048256.000	3	22682752.000	3.142	.065
S-Within	86638969.000	12	7219913.000		
B	143063040.000	4	35765760.000	15.283	.001
AB	85169728.000	12	7097477.000	3.033	.003
BS-Within	112334368.000	48	2340299.000		

ANALYSES OF VARIANCE - KJERSTAD DATA NON-RUNNERS EXCLUDED

Anova of Body Weight

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	6862.281	4	1715.570	1.309	.318
S-Within	17044.000	13	1311.077		
B	15421.770	4	3855.442	77.979	.001
AB	1106.030	16	69.127	1.398	.180
BS-Within	2571.00	52	49.442		

Anova of Food

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	112.297	4	28.074	1.953	.161
S-Within	186.885	13	14.373		
B	26.578	4	6.645	3.883	.008
AB	53.712	16	3.357	1.962	.035
BS-Within	88.997	52	1.711		

Anova of Wheel Running

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	109287200.000	3	36429056.000	13.291	.001
S-Within	27409808.000	19	2740980.000		
B	191842016.000	4	47969496.000	40.687	.001
AB	134177376.000	12	11181448.000	9.486	.001
BS-Within	47151216.000	40	1178780.000		

ANALYSES OF VARIANCE - LAST 5 DAYS DATA, ALL ANIMALS INCLUDED

Anova of Body Weight

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	11725.000	4	2931.250	1.704	.201
S-Within	25799.000	15	1719.933		
B	4380.000	4	1095.000	20.178	.001
AB	1179.000	16	73.688	1.358	.194
BS-Within	3256.000	60	54.267		

Anova of Food

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	130.254	4	32.563	1.286	.319
S-Within	379.684	15	25.312		
B	24.884	4	6.221	3.239	.018
AB	28.118	16	1.757	.915	.557
BS-Within	115.246	60	1.921		

Anova of Wheel Running

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	147218880.000	3	49072960.000	3.860	.038
S-Within	152557312.000	12	12713109.000		
B	115230144.000	4	28807536.000	12.753	.001
AB	63629184.000	12	5302432.000	2.347	.018
BS-Within	108427520.000	48	2258906.000		

ANALYSES OF VARIANCE - LAST 5 DAYS DATA, NON-RUNNERS EXCLUDED

Anova of Body Weight

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	3912.134	4	978.033	.889	.498
S-Within	14302.000	13	1100.154		
B	5183.160	4	1295.790	28.588	.001
AB	1542.574	16	96.411	2.127	.021
BS-Within	2357.000	52	45.327		

Anova of Food

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	183.363	4	45.841	2.534	.091
S-Within	235.215	13	18.093		
B	23.705	4	5.926	3.369	.016
AB	40.380	16	2.524	1.435	.163
BS-Within	91.480	52	1.759		

Anova of Wheel Running

Source	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	Prob.
A	239901168.000	3	79967056.000	23.505	.001
S-Within	34020608.000	10	3402060.000		
B	152939408.000	4	38234848.000	25.694	.001
AB	98175120.000	12	8181260.000	5.498	.001
BS-Within	59524096.000	40	1488102.000		

APPENDIX F

NONADJUSTED MEANS FOR DEPENDENT MEASURES

NONADJUSTED MEANS FOR WEIGHT (grams)

Table A
Kjerstad Data

Group	Control	2HR	6HR	12HR	23HR
Time 1	227.00	216.00	205.50	213.25	244.25
2	219.50	205.25	197.75	202.25	230.00
3	211.00	197.25	190.00	194.75	226.00
4	203.00	188.75	181.25	186.25	217.00
5	200.50	183.75	168.75	175.75	198.50

Table B
Kjerstad Data, Non-runners Excluded

Group	Control	2HR	6HR	12HR	23HR
Time 1	227.00	216.00	205.50	217.33	233.33
2	219.50	205.25	197.75	207.00	219.00
3	211.00	197.25	190.00	199.33	216.00
4	203.00	188.75	181.25	188.33	205.00
5	200.50	183.75	168.75	175.00	179.33

NONADJUSTED MEANS FOR WEIGHT (grams)

Table C
Last 5 Days Data

Group	Control	2HR	6HR	12HR	23HR
Time 1	207.00	195.50	199.75	192.50	224.75
2	203.25	193.50	194.75	190.50	222.75
3	202.25	190.25	187.25	187.50	214.50
4	200.50	187.25	179.50	182.25	206.75
5	200.50	183.75	168.75	176.25	198.25

Table D
Last 5 Days Data, Non-Runners Excluded

Group	Control	2HR	6HR	12HR	23HR
Time 1	207.00	195.50	199.75	196.66	214.33
2	203.25	193.50	194.75	194.66	212.33
3	202.25	190.25	187.25	190.00	201.33
4	200.50	187.25	179.50	183.66	191.66
5	200.50	183.75	168.75	175.00	179.00

NONADJUSTED MEANS FOR FOOD INTAKE (grams)

Table E
Kjerstad Data

Group	Control	2HR	6HR	12HR	23HR
Time 1	9.87	8.70	6.75	8.07	7.57
2	9.97	9.77	8.07	10.00	9.17
3	10.40	8.82	9.52	9.70	10.47
4	11.47	9.80	8.35	9.87	8.57
5	11.10	9.67	6.12	9.35	7.40

Table F
Kjerstad Data, Non-runners Excluded

Group	Control	2HR	6HR	12HR	23HR
Time 1	9.87	8.70	6.75	8.26	6.80
2	9.97	9.77	8.07	9.40	8.40
3	10.40	8.82	9.52	9.20	9.76
4	11.47	9.80	8.35	9.23	7.03
5	11.10	9.67	6.12	9.23	5.33

NONADJUSTED MEANS FOR FOOD INTAKE (grams)

Table G
Last 5 Days Data

Group	Control	2HR	6HR	12HR	23HR
Time 1	11.00	11.40	8.00	9.57	10.42
2	11.50	9.52	8.95	9.27	8.47
3	11.05	10.45	8.65	8.87	8.77
4	11.85	10.07	8.20	9.47	9.35
5	11.10	9.60	6.12	8.75	7.40

Table H
Last 5 Days Data, Non-runners Excluded

Group	Control	2HR	6HR	12HR	23HR
Time 1	11.00	11.40	8.00	9.16	9.83
2	11.50	9.52	8.95	9.16	7.06
3	11.05	10.45	8.65	9.06	7.20
4	11.85	10.07	8.20	9.40	7.23
5	11.10	9.60	6.12	9.23	5.33

NONADJUSTED MEANS FOR RATE OF WHEEL RUNNING (turns/hour)

Table I
Kjerstad Data

Group	2HR	6HR	12HR	23HR
Time 1	59.50	32.75	14.50	10.75
2	69.25	33.00	27.50	21.50
3	108.75	53.25	49.75	49.75
4	107.00	246.00	103.75	210.00
5	182.75	598.50	273.00	326.50

Table J
Kjerstad Data, Non-runners Excluded

Group	2HR	6HR	12HR	23HR
Time 1	59.50	32.75	19.00	9.33
2	69.25	33.00	36.00	14.33
3	108.75	53.25	65.00	36.33
4	107.00	246.00	138.00	143.33
5	182.75	598.50	363.33	302.66

NONADJUSTED MEANS FOR RATE OF WHEEL RUNNING (turns/hour)

Table K
Last 5 Days Data

Group	2HR	6HR	12HR	23HR
Time 1	38.25	35.00	26.50	30.75
2	54.25	49.00	54.25	67.50
3	91.75	71.00	120.25	204.50
4	117.00	274.50	188.50	222.50
5	180.75	598.50	272.75	326.50

Table L
Last 5 Days Data, Non-runners Excluded

Group	2HR	6HR	12HR	23HR
Time 1	38.25	35.00	35.00	40.66
2	54.25	49.00	71.66	89.[illegible]
3	91.75	71.00	160.00	272.33
4	117.00	274.50	250.66	296.33
5	180.75	598.50	363.33	434.66