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THE UNIVERSITY OF ALBERTA

"SELF-STARVATION" IN RATS AND MICE

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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DEPARTMENT OF PSYCHOLOGY

EDMONTON, ALBERTA
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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "SELF-STARVATION" IN RATS AND MICE submitted by LARRY STEFAN in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in PSYCHOLOGY.

Wm F Epling
Supervisor

W. David Pierce

Date July 16, 1980

Dedication

To Frank and Dave who provided the stimulus, and to Sheila who provided the reinforcement.

Abstract

This study used a factorial design to demonstrate that rats and mice restricted to a daily feeding of 1 hr. and 3 hr. respectively and allowed access to a wheel dramatically increased wheel-running, reduced food intake, and were unable to maintain weight ("self-starvation"). Control subjects on the same daily feeding schedule but with no access to a wheel were able to stabilize body weight and ingest more food. The results are discussed in terms of schedule-induced behavior.

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Acknowledgement

A note of appreciation is offered to the members of the operant seminar group for their helpful comments on this research.

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Chapter Page

Introduction

Routtenberg and Kuznesof (1967) found that rats fed 1 hr. per day in a home cage would stabilize body weight, but if access to a wheel were permitted the animals would dramatically increase activity, reduce food intake, and lose weight until death overtook them. The authors labelled this phenomenon "self-starvation".[1] The aim of the present study is to futher investigate this paradoxical effect by replicating Routtenberg and Kuznesof's (1967) study, using a factorial design and extending the findings to mice.

In one of Routtenberg and Kuznesof's (1967) series of five experiments they fed 36 rats 45-60 min. each day for 9 days and then 30 min. a day thereafter. Experimental subjects were given access to a wheel and restricted to a side cage either 1 hr. before, 2 hr. before or 2 hr. after the daily feeding. All 30 experimental subjects "self-starved", while the 6 control subjects living in home cages stabilized weight and survived. Weight stabilization was defined as the weight on Day 4 of any 4 day period being equal to or greater than the weight on Day 1 of that 4 day period. Concomitant with the experimental subjects' steady decline in body weight was a progressive rise in

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[1] The use of the term "self-starvation" in Routtenberg and Kuznesof's (1967) experiment and in the present study does not imply a "willingness" by the animal to restrict food intake. Rather it refers to a phenomenon involving the reciprocal effects of high activity and reduced food consumption. The concept is used to distinguish between starvation as described in this study and starvation that could be generated by the simple restriction of food.

wheel-running, except for the last day when death occurred. Moskowitz (1959) using similiar experimental conditions has reported the same negative correlation between body weight and activity in rats (r= -.99).

In another experiment Routtenberg and Kuznesof (1967) divided 15 experimental subjects into 3 groups of 5 rats each of which was fed for either 30, 45, or 60 min. a day. All 15 subjects had access to a wheel except during the feeding period and up to 1 hr. before when they were restricted to a side cage. The results revealed a significant reduction of food intake for each experimental group compared to a control group housed in a home cage without access to a wheel. Once again wheel-running was found to increase dramatically during the experiment. Since death was quite predictable a day or two before it occurred, subjects which ate less than 1 gm. during the feeding period were sacrificed to avoid unnecessary suffering. Using the starvation index and the weight stabilization criterion it was found that all experimental and control subjects in the 30 min. feeding group starved; all experimental and 4 out of 5 of the control subjects in the 45 min. group starved; and 4 out of 5 of the experimental and 1 of the 5 control subjects starved in the 60 min. group. These results suggest that the majority of rats with a wheel and 1 hr. access to food each day will self-starve.

Routtenberg (1968) further investigated the phenomenon of self-starvation and was able to label two variables that result in a decrease in food intake. One variable, novelty stress, was considered to be due to a change to a new environment, e.g. placing a rat formerly housed in a home cage into a wheel apparatus. The effect of novelty stress was to reduce food intake, but only for a few days. The other variable, deprivation stress, was said to be due to the effects of running in combination with a restricted food schedule. Unlike novelty stress, which dissipated in a few days, the effects of deprivation stress did not abate and it was therefore considered to be the crucial factor in "self-starvation".

The above studies indicate that rats need at least 1 hr. of access to food a day when housed in home cages in order to maintain weight and that novelty stress if present dissipates in a few days and is not crucial to self-starvation. Self-starvation appears to be the result of increased wheel-running concomitant with reduced food intake.

Though Routtenberg and Kuznesof (1967) have convincingly demonstrated that "self-starvation" is a reliable phenomenon, their studies employed a design that was incomplete. A complete factorial design can yield interesting interactions which may help to unravel the determinants of the phenomenon. In addition to the food-restricted groups employed by Routtenberg and Kuznesof (1967) a complete factorial design would have to include groups receiving ad lib food with or without access to a wheel. It is important to control for other systematic effects which might cause increased wheel-running, e.g. "learning to run". If rats on ad lib food and with access to a wheel show increased running over consecutive days this would weaken the argument that food-restriction per se is the reason for heightened wheel-running.

The other group, ad lib food and no wheel, is important to complete the factorial design so that interaction effects can be studied. For the above reasons it is considered necessary to do a systematic replication of Routtenberg and Kuznesof's (1967) study using a complete factorial design.

It is interesting to note that Routtenberg and Kuznesof's (1967) "self-starvation" in rats involves the non-contingent presentation of food after an extended interval. This fixed food schedule is similiar to that used in experiments on schedule-induced behaviors, where small portions of a meal are usually presented about every 60-180 seconds. This sort of schedule has been found to produce exaggerated and excessive stereotypic behaviors such as polydipsia, pica, attack, etc. (Falk, 1971). The distribution of food in Routtenberg and Kuznesof's (1967) experiment does not correspond exactly to that employed in the schedule-induced research. Instead, Routtenberg and Kuznesof (1967) gave their animals free access to food all at once after an extended interval of 23 hours. Thus a rat may obtain a single food pellet after a couple of minutes as in schedule-induced research or it may obtain its entire food ration for the day at the end of an extended time period. In both cases, however, it is important to note that excessive activity is generated and maintained. This may reflect the fact that in self-starvation and schedule-induced experiments porportionality between the amount of food delivered and the length of the food interval remain the same.

There are other similarities between Routtenberg and Kuznesof's (1967) investigation of self-starvation and schedule-induced experiments. A particular concern for the present study is the controlling function of specific stimulus events in the situation (Wayner, 1974). The presence of a stimulus such as a licking tube or another animal is critical in specifying and controlling the particular schedule-induced behavior which occurs. Thus rats given a drinking tube engage in excessive drinking and those exposed to a conspecific engage in attack. In self-starvation research, the presence of a running wheel, as a specific stimulus event, generates excessive running rather than other activities like grooming or attack. It would appear that the use of an environmental stimulus such as a wheel allows high activity which is essential to weight loss.

A plausible account of the relationship between schedule-induced literature and self-starvation comes from Collier, Hirsch, and Kanarek (1977). This series of investigations has provided evidence in support of the notion that behavior generated by long food intervals where an organism may receive an entire meal is similiar to but not identical with behavior maintained by typical operant research strategies. This self-starvation study employs long food intervals and analyzes behavior between meals while the schedule-induced experiments use a paradigm that employs a short food interval, and behavior within a single meal is investigated. Collier et al. (1977) propose that analyzing behavior between large food presentations at relatively long intervals suggests new variables that reflect the structure of the animal's natural environment.

This study also extends the "self-starvation" phenomenon to mice to test the hypothesis that the findings are not specific to the rat species. Cornish and Mrosovsky (1965) conducted a study of deprivation and activity in six different species of rodents. Since food restriction consisted of 3 days of total deprivation the results are not directly comparable to Routtenberg and Kuznesof's findings. However, Cornish and Mrosovsky did find that in the face of food deprivation non-hiberators (rats and guinea pigs) increased activity, as measured on a wheel, while hibernators (dormice, ground squirrels, and chipmunks) suspended activity and went into hibernation.[2]

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[2] One rodent, the hamster, although an animal capable of hibernation, increased its running instead. The authors account for this behavior by the fact that a hamster does not easily enter hibernation unless an adequate food supply is stored.

Cornish and Mrosovsky's study would indicate that non-hibernators faced with food restriction increase activity. Thus it would be expected that the white mouse, a non-hibernating rodent like the rat, would also increase activity during food restriction and demonstrate a similiar "self-starvation" effect. It should be noted that since a mouse's body size is small, its metabolism is consequently higher than that of a rat. For this reason the present study allows mice 2 hr. longer to feed than rats so that they may have an equal opportunity to stabilize their body weight on food restriction.

Hypotheses

1. Subjects on food restriction and with access to a wheel will increase wheel running, reduce food intake and decline in weight more than subjects with food restriction and no wheel or subjects on ad lib food with or without access to a wheel.

Since heightened activity levels are considered to suppress food intake it is expected that subjects on food restriction and access to a wheel will ingest less food than subjects on food restriction and no wheel. Subjects on food restriction and access to a wheel are expected to self-starve. Subjects on food restriction and no wheel should stabilize weight. Subjects in ad lib conditions with or without a wheel are expected to have comparable food intake and weight gains in accordance with normal growth.

2. The effects of "self-starvation" as detailed in Hypothesis 1 are expected to be found in both rats and mice.

Method

Subjects: 16 Alas strain mice 27 days old and 16 Sprague-Dawley rats 41 days old were used. All subjects were males.

Apparatus: 8 standard Wahman activity wheels with a 25 x 15 x 12 cm. side cage equipped with a sliding door for access to the wheel were used for the rats. 8 smaller activity wheels with an 11 x 5 x 6 cm. side cage were used for the mice. The side cage could be moved to prevent entrance to the wheel. The rat wheels were 35 cm in diameter and 11 cm in width, while those for the mice were 15 cm in diameter and 5 cm in width. All activity wheels were equipped with counters which recorded wheel revolutions regardless of the direction of turn. Non-wheel subjects were maintained in standard plastic cages (45 x 24 x 20 cm. for rats; 28 x 18 x 12 for mice) filled to approximately 3 cm with pine sawdust and covered with a wire lid that held food and water.

Procedure: On arrival all subjects within each species were assigned with the use of a random number table to one of the following 4 groups.

WD = access to wheel while on food deprivation
WA = access to wheel while on ad lib food
NWD = no wheel while on food deprivation
NWA = no wheel while on ad lib food

After a 5 day baseline of weight and ad lib food intake WD and WA were placed in a wheel and the predetermined feeding schedule for each group was instituted.

The deprivation rats (WD and NWD) were fed for 1 hr a day while the deprivation mice (WD and NWD) were allowed 3 hr. access to food. During the feeding period WD of each species was prevented access to the wheel. All subjects were weighed immediately prior to their feeding at 6:30 p.m. For rats, weight and food consumption were measured to an accuracy of 0.5 gm while for mice accuracy was 0.1 gm. Food was standard Purina rat chow in bar form. All Ss were on ad lib water.

Subjects were kept on their schedules until the starvation or stablization criterion was met. Starvation criterion was defined as 70% or less of pre-experimental weight. Weight stabilization criterion was the same as used by Routtenberg and Kuznesof (1967): on day 4 of any consecutive 4 day period weight is equal to or greater than that of day 1.

Results

Prior to the main analysis an analysis of variance was conducted on body weights for the last day of the pre-experimental period to see if any of the groups differed significantly in weight. This analysis showed that the mouse groups were nearly significantly different with regard to pre-experimental body weight ($P<.068$). The rat groups were more homogeneous ($P<.567$), but because of the large variation in body weight among the mouse groups it was deemed necessary that the analysis used on body weight for criterion day should take into account pre-experimental weights. It was for this reason that an analysis of covariance on body weights for each species (rats were included to keep the type of analysis consistent between the species) was conducted on the criterion day weight. Pre-experimental body weight was the co-variate and treatment condition was the factor. Since the remainder of the study was concerned with the experimental effects over time, an analysis of variance on activity by food restriction was conducted with proportion of time to criterion as a repeated measure.

A problem was encountered in how the data should be analyzed. Subjects of both species in WD met starvation criterion in 4 to 6 days less than NWD subjects took to meet weight stabilization criterion. Essentially then, the problem was that while the time to criterion varied from subject to subject, equal data points were necessary in the analysis. Routtenberg and Kuznesof (1967) encountered the same problem and dealt with it by analyzing the last days from criterion. In their study one subject completed the experimental phase in 8 days, thus only the last 8 days of the experimental phase for all subjects were analyzed. This type of analysis seemed inappropriate for the present study. The data collected from subjects who took longer to meet a criterion were deemed important and therefore should somehow be included in the analysis. The inappropriateness of only analyzing the last days to criterion was most striking in view of the fact that a couple of mice met criterion in 2 days and thus only the last 2 days of all mouse data could be used. Using only the last 2 days of data would not adequately reflect what was happening over the whole experimental phase.

An alternative technique for analyzing the data was to use a method first employed by Vincent (1912).[3] The technique was developed for experiments where trials to criterion varied widely among subjects. A close look at Kjerstad's variation of the Vincent technique as outlined by Hilgard (1938) suggested that this method was superior to analyzing the last days from criterion. Basically, the technique involves dividing each subject's total number of days to criterion into fractional parts. For example, since 2 rats met a criterion in only 4 days all of the rat data for each subject were divided by the process of simple

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[3] The author is indebted to Dr. Don Heth for suggesting this method.

interpolation into 4 time portions with data on criterion day always being the last time portion. Since 2 mice met criterion in 2 days all mouse data were Vincentized into 2 time portions. This method made it possible to combine data for subjects whose times to criterion were widely different. This also satisfied the need to include data from the first days of the experimental phase for subjects who took longer to reach a criterion. For rats each of the 4 time portions can be viewed as 25% to criterion, thus time portion 1 reflects where all rats stand with regard to weight, food intake and wheel-running 25% of the way to criterion. For mice only 2 time portions are used, thus each can be viewed as 50% of criterion.

Criterion Analysis

As predicted in Hypothesis 1 all subjects allowed access to a wheel and on food restriction (WD) met the starvation criterion in 4 to 5 days for rats and 2 to 3 days for mice. No subjects on food restriction without a wheel (NWD) "self-starved", and all were able to ingest enough food to stabilize body weight; rats in 8 days, mice in 7 to 8 days. All other subjects with the exception of one mouse (S no. 5) in WA maintained or increased their weight over the experimental phase. The one mouse in WA, in spite of ad lib food, increased its running over a 5 day period while steadily dropping in weight till starvation criterion was met. A Fisher Exact Test (Segal, 1950) conducted on the criterion outcome for rats showed the results to be significant (P<.014). For mice, in spite of one mouse's "self-starvation" while on ad lib food, the results were also found to be significant (P<.05).

Weight

There was a significant food restriction by wheel interaction over time in rats (F=17.56 df=3,36 P<.001). (See Appendix A for the breakdown of all analyses of variance and covariance and Appendix B for Scheffe tests on group means.) An analysis of covariance conducted on criterion weights with pre-experimental weight as the covariate and treatment as the factor revealed significant effects for the covariate (F=340.0 df=1,11 P<.001) and the treatment (F=513.66 df=3,11 P<.001). A Scheffe analysis (alpha=.05) on the group means in Table 1 showed that rats in WD (food restriction and access to wheel) weighed significantly less on criterion day than NWD (food restriction and no wheel) rats. The Scheffe analysis revealed that rats in a wheel and on ad lib food (WA) weighed significantly less than rats on ad lib food but with no wheel (NWA) (alpha=.05). This table also shows that WD rats steadily declined in body weight over the experimental phase until starvation criterion was met. Subjects on food restriction but no wheel were able to stabilize and rats in both ad lib conditions continued to make comparable weight gains over the course of the experimental phase. It is interesting to note that WA rats (ad lib food and access to wheel) had a lower body weight than ad lib food but no wheel rats (NWA). This would indicate that rats which engage in mild to moderate exercise have lower body weights than rats without an opportunity to exercise.

Examination of the mouse data in Table 2 reflects essentially the same finding as in rats. There was a highly significant food restriction by wheel interaction found over time (F=48.78 df=1,11 P<.001). Unlike the rats there was no significant difference in the group weights on criterion day between WD and NWD or between WA and NWA.

For subjects of each species with food restriction and access to a wheel, an inverse relationship was found between weight and wheel-running; for rats r= -.90, and for mice r= -.85.

Food Intake

Analysis of variance conducted on food intake in rats revealed a significant food restriction by wheel over time interaction (F=3.24 df=3,36 P<.033). An analysis of variance on the food intake for rats on criterion day showed a significant difference between the groups (F=306.44 df=3,12 P<.001). A Scheffe analysis (alpha=.05) on the group means reported in Table 3 revealed a significant difference on criterion day for food intake between rats on food restriction with access to a wheel (WD) and rats on food restriction but with no wheel (NWD). There was no significant difference in food intake between WA and NWA. This supports the idea that heightened activity functions to suppress food intake.

Analysis on food ingestion in mice shows the same significant interaction effects as found in rats (F=11.08 df=1,11 P<.007). An analysis of variance conducted on the food intake for mice on criterion day revealed a significant difference between the groups (F=17.66 df=3,12 P<.001). A Scheffe analysis (alpha=.1)[4] on food intake means reported in Table 4 found that on criterion day, as in rats, WD mice ate significantly less than NWD mice. Once again this would indicate that heightened activity serves to suppress food-intake. Though WD mice did eat less on the criterion day than during the first time period, this was not significant using the Scheffe analysis (alpha=.1).

Activity Effects

It can be seen in Table 5 that rats which had access to a wheel and were food restricted (WD) dramatically increased wheel-running over the experimental phase while rats on ad lib food with a wheel (WA) did not increase their running, but maintained a low daily run of a few hundred revolutions. This wheel-running by deprivation over time was significant (F=16.38 df=3,18 P<.001).

Data for the mice did not confirm this portion of Hypothesis 1; wheel-running was not significantly different between the WD and WA groups (F=2.29 df=1,6 P<.181). A likely explanation for this was that one mouse in WA increased its running over the experimental phase while

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[4] Due to the extreme conservatism of a Scheffe analysis, Scheffe (1953) recommends that alpha=.1 can legitimately be used in declaring a significant difference.

steadily dropping in weight till starvation criterion was met. Data from research conducted since the present experiment indicate that this mouse's "self-starvation" was atypical under the conditions employed. As it was deemed necessary to have data that properly characterized this group the data for this mouse were omitted and another analysis was conducted. This analysis confirmed Hypothesis 1; wheel-running was significantly greater in food restricted mice than mice fed ad lib (F=7.15 df=1,5 P<.044), but there was no significant interaction over time (F=6.38 df=1,5 P<.053).

Summary

The results predicted in Hypothesis 1 were found in the rat, thus replicating the "self-starvation" phenomenon in this species as stated in Hypothesis 2. Mice in this study that were food restricted and had access to a wheel (WD) also decreased in body weight, reduced food intake and increased wheel-running. This lends support to the extension of the "self-starvation" phenomenon to mice.

Table 1

Mean Weight per Period For Rats (gm)

	Time Periods			
Group	1	2	3	4
1	197.8	174.5	159.8	142.0
2	200.2	195.8	206.2	217.3
3	179.2	162.8	152.8	156.8
4	209.2	221.2	231.0	243.0

Table 2

Mean Weight per Period For Mice (gm)

	Time Periods	
Group	1	2
1	25.4	20.1
2	28.5	28.9
3	21.5	21.4
4	28.6	29.4

Table 3

Mean Food Consumption per Period For Rats (gm)

	Time Periods			
Group	1	2	3	4
1	5.2	5.0	5.8	3.6
2	24.8	26.2	25.8	26.0
3	5.5	6.3	7.8	8.0
4	25.0	24.2	25.2	26.1

Table 4

Mean Food Consumption per Period For Mice (gm)

	Time Periods	
Group	1	2
1	2.2	1.6
2	6.3	5.5
3	3.4	3.8
4	6.4	6.1

Table 5

Mean Number of Wheel Revolutions Per Period for Rats

	Time Periods			
Group	1	2	3	4
1	1117	2177	5606	8408
2	695	313	429	674

Table 6

Mean Number of Wheel Revolutions Per Period for Mice

	Time Periods	
Group	1	2
1	12525	19638
2	6964	10895
(2	7488	15468)[5]

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[5] With mouse no. 5 ommitted.

Discussion

This study confirmed Routtenberg and. Kuznesof's (1967) finding that rats on a food restriction schedule and with access to a wheel "self-starved", while rats on food restriction only stabilized in body weight. This "self-starvation" in rats was accompanied by higher wheel-running and lower food intake. The phenomenon was successfully extended to mice which also showed significantly higher wheel-running and lower food ingestion on the last day than their controls.

The finding that both rats and mice with access to a wheel while on food restriction show lower food intake than subjects without a wheel but still food restricted suggests that wheel-running in food restricted animals functions to futher suppress food intake. This is similiar to the finding of Stevenson, Box, Feleki, and Beaton (1966) who were able to demonstrate that rats on regular enforced running had lower food intake during that time period. The authors also investigated the effects of irregular bouts of enforced treadmill or swimming exercises. The findings was always the same: decreased food consumption on the day of enforced exercise.

There is evidence to suggest that this paradoxical phenomemon of decreased food intake on days of exercise can also be extended to man. Edholm, Fletcher, Widdowson, and McCance (1955) in a study on energy expenditure and food intake in cadets found that on days of military drilling when energy expenditure was the highest, caloric intake for that day was found to be significantly depressed in comparison to lower activity days.

The above studies both investigated enforced activity whereas in the present study all activity is voluntary. Levitsky (1970), in a study that involved voluntary wheel-running in rats, noted that the presence of a wheel resulted in decreased food consumption for 4 to 6 days. Levitsky also found that over a 17 day period the presence of a wheel resulted in a decrease in meal frequency. It is thus seen that even voluntary activtity in rats initially affects the amount of food consumed and has the long term effect of disturbing the normal frequency of meal eating.

The present study did not find a significant difference in food consumption between WA and NWA groups even though the former did weigh significantly less than the latter in both species. It should be remembered that this experiment used a 4-day stabilization criterion which these subjects easily attained. If the schedule were to be continued for several more days and/or slightly larger groups used it is expected that Levitsky's (1970) finding would have been confirmed.

It is of interest to note that Levitsky's (1970) rats which voluntarily ran in a wheel also voluntarily decreased their meal frequency. The present study and also that of Routtenberg and Kuznesof (1967) suggest that if meal frequency is experimentally decreased to only 1 meal a day a corresponding increase occurs in activity. The increase in activity in itself may not be particulary hazardous to the animal but as Stevenson et al. (1965), Routtenberg and Kuznesof (1967), and the present study have found, increased activity also causes a decrease in food consumption. This brings the animal into a predicament where it is unable to maintain weight, eventually leading to "self-starvation".

Like that of Moskowitz (1959) this study found that wheel-running and weight are inversely correlated. Opportunity to wheel-run appears to be crucial for self-starvation, but it is still a puzzle why an animal should increase its activity when food deprived. An evolutionary hypothesis suggests that an animal is more likely to come into contact with food if activity increases under deprivation conditions. Thus wheel-running or activity in general may be a survival mechanism which allows adaptation under conditions of deprivation. Futher indirect support for this contention is found in research which showed that non-hibernators increased their activity when deprived but hibernators did not (Cornish & Mrosovsky, 1965). This suggests that when a non-hibernator is deprived of food, since the option of hibernating is not available to him, his best choice from a survival point of view is to become active in search of food. More extensive research and theory which also involved evolutionary mechanisms as explanatory devices has been been offered by Staddon and Simmelhag (1978) and Falk (1977). Their research suggests that wheel-running, as seen in this study, may be related to what has been referred to in recent literature as adjunctive or interim behavior (Falk,1970,1977; Staddon & Simmelhag, 1978).

Staddon and Simmelhag (1971) have challenged Skinner's account of "superstitious" behavior. On typical short FI or VI schedules known to produce such behavior Staddon and Simmelhag have observed that behaviors immediately before and after the delivery of a primary reinforcer are distinctly different. The authors have labelled the behavior immediately after the reinforcer "interim" behavior and have noted that it appears to be inappropriate to the situation. Behavior before the reinforcer seems to be more appropriate to the conditions imposed on the animal. The subject engages in these behaviors until reinforcement is delivered, hence the label terminal behavior. Interim behavior is activity the organism engages in when food reinforcement is of low probability while terminal behavior occurs when reinforcement is at high probability. For example, a food deprived pigeon on an FI 18 sec. schedule will, after food reinforcement, engage in behaviors such as turning or wing flapping. These behaviors seem inappropriate to food eating and are often of considerable strength and persistence. As the inter-reinforcement interval proceeds the pigeon stops these behaviors and engages in activities such as standing close to the food magazine and/or pecking. These behaviors seem appropriate to eating food and are continued till food appears.

Staddon and Simmelhag (1971) proposed that interim behaviors have an evolutionary base. Interim behavior is thought to suppress terminal behaviors when the probability of reinforcement is low. The authors state "that natural selection will have fostered the development of a mechanism to ensure that animals avoid places at times, when on the basis of the past, they have learned that reinforcement is not forthcoming." (p. 38). Thus Staddon and Simmelhag have proposed that in the wild interim behavior functions to ensure that the animal leaves the situation to seek other reinforcers, but that in the confines of the lab this is prevented, resulting in heightened interim activity.

Application of Staddon and Simmelhag's (1971) theory to the findings of the present study would indicate that wheel-running may be of the same nature as the interim behavior observed on short schedules of reinforcment. In other words it can be argued that rats and mice in this study were on a once every 23 hr. (21 hr. for mice) schedule of food reinforcement. The resulting wheel-running can be viewed as interim behavior that is directly controlled by the food restriction schedule.

Staddon and Simmelhag point out that adjunctive behaviors as defined and researched by Falk (1971, 1977) are essentially interim behaviors. Falk defines adjunctive behavior as "behavior that is maintained at a high probability by stimuli which derive their exaggerated reinforcing efficacy primarily as a function of schedule parameters governing the availability of another class of reinforcing events." (1977, p.325). An example of adjunctive behavior is found in schedule-induced polydipsia where an animal forced to eat its meal in small spaced portions will often drink up to half its body weight in water during a 3 hr. session. The short schedules producing adjunctive behavior and its excessiveness and persistance are also those which produce Staddon and Simmelhag's interim behaviors. Falk (1977) also proposes an evolutionary mechanism to account for such behavior. His basic tenet is that adjunctive behavior keeps the subject in proximity to the intermittent reinforcer until temporal mediation resolves the situation and the reinforcer is once again available. Falk also addresses the strong similiarities between adjunctive behavior and displacement activities. Displacement behavior is observed in the wild when a strong drive is blocked, e.g. a male Zebra finch if threatened will suddenly start feeding if food is nearby or sexually mount a female if one is present, or if neither food nor a female is available, it will preen, or assume a sleeping posture. An important thing to note is that displacement behavior in the wild and adjunctive behavior in the lab are greatly modified by the stimuli present in the environment. Thus depending on the appropriate environmental stimuli presented excessive activities such as polydipsia, airlicking, pica, aggression, etc. have been produced in the lab (Falk, 1971). Falk's

(1971, 1977) research, which employs short intermittent reinforcement schedules like those used by Staddon and Simmelhag (1971), also indicates that self-starvation, as seen in this study, may be the consequence of the schedule of feeding and an appropriate environmental stimulus, in this case a wheel. Falk (1977) also predicts that the more spatially constrained a situation is, the greater the intensity of adjunctive behavior. Future research may further substatitate the claim that wheel-running is schedule-induced by varying the experimental space available to the animal. If the animal increased its wheel-running due to decreased available space this would be in accordance with Falk's (1977) prediction. This sort of outcome would also lend support to Staddon and Simmelhag's (1971) theory that the function of schedule-induced behavior is to remove the subject from the situation. Thus if a smaller space is used the animal would be less able to seek reprieve from the situation and more intense schedule-induced behaviors would be expected. Falk (1971, 1977) and Staddon & Simmelhag (1971) appear to be investigating the same phenomenon, and essentially making the same predictions. Their theories, based on a wide range of observations, may greatly increase the understanding of animal and human behavior. It is thus argued that the effects of activity, as seen in this study, should be guided by research and theory of adjunctive and interim behavior.

Evidence to further support the claim that wheel-running is a schedule-induced behavior has been reported by several researchers. Falk (1971), Staddon and Simmelhag (1971), and Wayner, Stein, Loullis, Barone, Jolicoeur, and Rondeau (1978) have all noted that body weight greatly influences the strength of schedule-induced behaviors. As body weight decreases schedule-induced behaviors increase in intensity and duration. The inverse relationship between activity and body weight in this study further supports the view that wheel-running is of the same nature as schedule-induced behaviors. Unfortunately for the animal wheel-running has the special effect of suppressing food intake resulting in "self-starvation".

The present research also has implications for the analysis of schedule-induced behavior. Most important in this regard is the connection suggested between an extended food-interval paradigm and the schedule-induced literature. In a summary of research, Collier et al. (1977) indicate that behavior can be generated and maintained by the presentation of entire meals after long temporal intervals. This behavior appears similar in nature to behavior generated and maintained by schedules of reinforcement where small portions of the meal are delivered in close temporal proximity. Thus, Collier et al. (1977) describe behavior that occurs between meal presentations while reinforcement analysts have concentrated on behavior occurring within the meal. Since reinforcement schedules are known to induce a variety of excessive behaviors (Falk, 1971, 1977; Staddon &

Simmelhag, 1971), Collier's et al. (1977) analysis of extended meal schedules would imply that schedule-induced behavior can occur even during lengthy food intervals. The research reported here and the findings of Routtenberg and Kuznesof (1967) and Routtenberg (1968) provide preliminary evidence for schedule-induced behavior generated by extended food intervals.

It can thus be seen that "self-starvation" can be explained in terms of schedule-induced behavior as investigated by Falk (1971, 1977), Collier et al. (1977), and Staddon & Simmelhag (1971). The wheel is an environmental stimulus which allows the organism to engage in activity. The side effect of activity is to decrease food intake. Decreased food intake in combination with increased activity lowers the animal's body weight which further increases activity. The reciprocal effects of these variables lead to "self-starvation".

In conclusion, this study was able to replicate the "self-starvation" phenomenon as observed by Routtenberg and Kuznesof (1967) and successfully extended it to the mouse species. It was further argued that the "self-starvation" phenomenon may be due to the effects of a special class of behaviors called adjunctive or interim and it is reccommended that future research be guided in accordance with these theories.

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Appendix A

Anova on Weight

Rats

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES	F RATIO	PROBABILITY
A	976.500	1.	976.500	0.831	0.380
B	39700.500	1.	39700.500	33.790	0.001
AB	2889.250	1.	2889.250	2.459	0.143
S-WITHIN	14099.000	12.	1174.917		
C	818.750	3.	272.917	37.500	0.001
AC	1258.250	3.	419.417	57.630	0.001
BC	9360.750	3.	3120.250	428.737	0.001
ABC	383.500	3.	127.833	17.565	0.001
CS-WITHIN	262.000	36.	7.278		

Mice

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES	F RATIO	PROBABILITY
A	1.990	1.	1.990	0.391	0.545
B	335.841	1.	335.841	65.937	0.001
AB	4.500	1.	4.500	0.883	0.367
S-WITHIN	56.027	11.	5.093		
C	8.236	1.	8.236	38.207	0.001
AC	14.091	1.	14.091	65.373	0.001
BC	19.962	1.	19.962	92.606	0.001
ABC	10.514	1.	10.514	48.779	0.001
CS-WITHIN	2.371	11.	0.216		

A=Wheel B=Food C=Time

Analysis of Covariance on Weight

Rats

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
COVARIATES	6052.246	1	6052.246	340.033	0.000
PREWT	6052.246	1	6052.246	340.033	0.000
MAIN EFFECTS	27427.699	3	9142.566	513.656	0.000
COND	27427.699	3	9142.566	513.656	0.000
EXPLAINED	33479.945	4	8369.984	470.250	0.000
RESIDUAL	195.789	11	17.799		
TOTAL	33675.734	15	2245.049		

Mice

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIGNIF OF F
COVARIATES	17.037	1	17.037	3.562	0.086
PREWT	17.037	1	17.037	3.562	0.086
MAIN EFFECTS	254.345	3	84.782	17.728	0.000
COND	254.345	3	84.782	17.728	0.000
EXPLAINED	271.382	4	67.846	14.186	0.000
RESIDUAL	52.607	11	4.782		
TOTAL	323.989	15	21.599		

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                         Anova on Food

                              Rats

SOURCE          SUM OF     DEGREES OF      MEAN          F
                SQUARES     FREEDOM       SQUARES      RATIO     PROBABILITY

  A               8.482        1.            8.482       1.566       0.235
  B            6101.555        1.         6101.555    1126.238       0.001
  AB             25.377        1.           25.377       4.684       0.051
   S-WITHIN      65.012       12.            5.418

  C              11.026        3.            3.675       3.691       0.021
  AC             14.371        3.            4.790       4.810       0.006
  BC              5.114        3.            1.705       1.712       0.182
  ABC             9.691        3.            3.230       3.244       0.033
   CS-WITHIN     35.852       36.            0.996


                              Mice

SOURCE          SUM OF     DEGREES OF      MEAN          F
                SQUARES     FREEDOM       SQUARES      RATIO     PROBABILITY

  A               7.822        1.            7.822      16.755       0.002
  B              80.825        1.           80.825     173.132       0.001
  AB              3.323        1.            3.323       7.118       0.022
   S-WITHIN       5.135       11.            0.467

  C               0.022        1.            0.022       0.122       0.734
  AC              0.013        1.            0.013       0.072       0.794
  BC              0.175        1.            0.175       0.987       0.342
  ABC             1.971        1.            1.971      11.085       0.007
   CS-WITHIN      1.956       11.            0.178

                     A=Wheel   B=Food   C=Time
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                        Anova on Food on Criterion Day

                                     Rats

                              SUM OF                MEAN              SIGNIF
SOURCE OF VARIATION          SQUARES     DF        SQUARE       F      OF F
MAIN EFFECTS                1827.482      3       609.161  306.444    0.000
   COND                     1827.482      3       609.161  306.444    0.000
EXPLAINED                   1827.482      3       609.161  306.444    0.000
RESIDUAL                      23.854     12         1.988
TOTAL                       1851.336     15       123.422


                                     Mice

                              SUM OF                MEAN              SIGNIF
SOURCE OF VARIATION          SQUARES     DF        SQUARE       F      OF F
MAIN EFFECTS                  57.531      3        19.177   17.664    0.000
   COND                       57.531      3        19.177   17.664    0.000
EXPLAINED           [illegible].531      3        19.177   17.664    0.000
RESIDUAL            [illegible].028     12         1.086
TOTAL                         70.559     15         4.704
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                              Anova on Wheel


                                   Rats

SOURCE            SUM OF     DEGREES OF       MEAN             F
                  SQUARES     FREEDOM        SQUARES         RATIO    PROBABILITY

  A            115447808.000     1.       115447808.000      25.614      0.002
   S-WITHIN     27043328.000     6.         4507221.000

  B             68209088.000     3.        22736352.000      17.168      0.001
 AB             65062080.000     3.        21687360.000      16.376      0.001
  BS-WITHIN     23838720.000    18.         1324373.000


                                   Mice

SOURCE            SUM OF     DEGREES OF       MEAN             F
                  SQUARES     FREEDOM        SQUARES         RATIO    PROBABILITY

  A             84580352.000     1.        84580352.000       2.290      0.181
   S-WITHIN    221599488.000     6.        36933248.000

  B            228092928.000     1.       228092928.000       7.606      0.033
 AB               732160.000     1.          732160.000       0.024      0.881
  BS-WITHIN    179922688.000     6.        29987104.000


                             Without Mouse No.5

SOURCE            SUM OF     DEGREES OF       MEAN             F
                  SQUARES     FREEDOM        SQUARES         RATIO    PROBABILITY

  A            175113616.000     1.       175113616.000       7.154      0.044
   S-WITHIN    122397184.000     5.        24479424.000

  B            104734976.000     1.       104734976.000       6.379      0.053
 AB              8733255.000     1.         8733255.000       0.532      0.499
  BS-WITHIN     82087424.000     5.        16417484.000

                               A=Food  B=Time
```

Appendix B

Scheffe Test On Group Means

Independent Variable	Species	Comparison on Criterion Day	t	t'(df)	Prob.
Weight	Rat	Group WD vs NWD	5.03	3.14 (3,15)	.05
		Group WA vs NWA	10.39	3.14 (3,15)	.05
	Mice	Group WD vs NWD	0.82	3.14 (3,15)	NS
		Group WA vs NWA	1.94	3.14 (3,15)	NS
Food	Rat	Group WD vs NWD	4.34	3.14 (3,15)	.05
		Group WA vs NWA	0.62	3.14 (3,15)	NS
	Mice	Group WD vs NWD	2.85	2.73 (3,15)	.1
		Group WA vs NWA	0.23	3.14 (3,15)	NS