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Wheel running, feeding, and body weight in adult male rats: Generalizations to adult females and younger animals

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Wheel Running, Feeding, and Body Weight in Adult Male Rats: Generalizations to Adult Females and Younger Animals

By

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Abstract

For adult male rats, initial access to a running wheel results in a pronounced suppression of feeding with a subsequent disruption of weight gain, but results with female and younger rats are not as clear. The present experiments demonstrated that age may be a confounding factor in the conflicting reports. The effects of ad lib wheel access on feeding and body weight were investigated in adult male, adult female, and weanling male rats using consistent procedures and recording data daily. For adult males and females, wheel access initially suppressed feeding and reduced weight relative to sedentary controls. These effects were similar in males and females. Weanling males displayed only a mild, temporary, feeding and weight suppression, which became non-significant when compared to the adult males. Thus, age seems to be an important factor in wheel running effects on feeding and weight. These age differences may speak to the age differences in incidence of anorexia nervosa.

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Wheel Running, Feeding and Body Weight in Adult Male Rats:

Generalizing to Adult Females and Younger Animals

Given the precise regulation of energy balance in animals and humans, it might be expected that if energy expenditure increased, food consumption would increase as well. Surprisingly, considerable research indicates that an initial temporary feeding suppression is observed in adult male rats with exposure to either forced treadmill running (Applegate, Upton & Stern, 1982; Eugene et al., 1969; Katch, Martin, & Martin, 1979; Nance, Bromley, Barnard, & Gorski, 1977) or voluntary wheel running (Cortright, Chandler, Lemon & DiCarlo, 1997; Jones, Bellingham, & Ward, 1990; Levitsky, 1970; Looy & Eikelboom, 1989; Pitts, 1984). As a function of this increased energy expenditure (i.e., exercise) and the decrease in energy intake (i.e., in feeding), exercising adult male rats either lose weight or gain weight more slowly than do their sedentary controls (Applegate et al., 1982; Cortright et al., 1997; Eugene et al., 1969, Goodrick, 1980; Hill, Davis, Tagliaferro, & Stewart, 1984; Jones et al., 1990; Katch et al., 1979; Levitsky, 1970; Looy & Eikelboom, 1989; Nance et al., 1977; Pitts, 1984; Pitts & Bull, 1977; Tokuyama, Saito, & Okuda, 1982).

The feeding and weight suppression seen in adult male rats when a running wheel becomes available embodies several characteristic features of anorexia nervosa in humans. In anorexia nervosa, food consumption is voluntarily decreased. Associated with this decrease in feeding is an increase in exercise that some have argued is an essential feature of the disorder (Yates, 1989). This combination of decreased energy intake and increased energy expenditure results in a rapid weight loss that can, in some cases, prove fatal. Thus, the ability of exercise to suppress feeding in rats has attracted some attention. In the extreme case, if food access in rats is restricted to a short period per day and the animal is given ad lib wheel access, food consumption is suppressed while running increases phenomenally. This combination (called activity anorexia) can lead to self-starvation and death (Routtenbourg & Kuznesof, 1967; Spear & Hill, 1962). While the feeding suppression may be more drastic if food is available for only one hour a day, the feeding suppression is also seen with ad lib feeding and wheel access.

Adult male rats have typically been used for many investigations of wheel-induced changes in feeding and body weight (Applegate et al., 1982; Eugene et al., 1969, Hill et al., 1984; Katch et al., 1979; Levitsky, 1970; Looy & Eikelboom, 1989; Nance et al., 1977; Pitts & Bull, 1977). However, the combination of feeding suppression observed with initial wheel access and the decreased weight evident with continuous wheel access, is not well understood. The present study examines whether the effect of wheel access on feeding and weight seen in **adult male** rats also occurs in **adult females** and **younger males**. Thus, this study tests the variables of sex and age in a wheel running paradigm. A cautionary note needs to be made about the age factor. Because weanlings are gaining weight rapidly, it may be the weight gain difference, rather than the age difference, which is responsible for any "age" effects found on feeding and weight gain. The rationale for this study will be developed through the following four sections. The first three sections describe wheel running and its effects on feeding and weight for adult males, adult females, and weanling males. The last section describes how previous studies differ from the methodology used in the present study.

Wheel Running, Feeding, and Weight in Adult Males

In adult male rats, wheel running increases from about 1 km a night over a few weeks until a plateau is reached of 5-10 km a night (Anantharaman-Barr & Decombaz, 1987; Cortright et al., 1997 Eikelboom & Mills 1988; Mondon, Dolkas, Sims & Reaven, 1985; Pitts, 1984). The variance of wheel running between rats is great: Some rats run at lower intensities (e.g., 1000 revolutions/night, approximately 1 km), while others run at extremely high intensities (e.g., 12, 000 revolutions/night). However, once a plateau is achieved, wheel running is relatively stable for each animal. This intensity of running behaviour continues for months before declining, as rats get older (Mondon et al., 1985; Pitts, 1984). Furthermore, animals find wheel running intrinsically rewarding. This is evidenced by the fact that animals will lever press to gain access to a wheel (Belke & Heyman, 1994; Iversen, 1993; Kagan & Berkun, 1954). Obviously any behaviour this prevalent and rewarding must be important to the animal, but no clear explanation for running exists (Sherwin, 1998).

Wheel running affects several aspects of energy balance in adult male rats including food intake, and weight regulation. As mentioned earlier, feeding is suppressed for several days at wheel introduction. The suppression with initial wheel access seems to be paradoxical. Running should result in an increased energy expenditure, and thus what would be expected is a compensation with an increased energy intake -- not the decreased food intake observed. Looy and Eikelboom (1989) investigated feeding and wheel access in non food-deprived male rats. They found a dramatic drop (40%) in food intake with wheel access, which recovered to control levels after two weeks of wheel exposure. Premack and Premack (1963) report that after 20 days of wheel access, removal of the wheel temporarily increased food intake. Both studies taken together suggest that feeding is affected by wheel access -- make a wheel available to a rat and food consumption decreases, while removing wheel access can result in feeding increases. The initial effects of wheel access on feeding in adult male rats have been replicated several times suggesting it is a robust phenomenon (Levitsky, 1970; Looy & Eikelboom, 1989; Mueller, Loft, & Eikelboom, 1997; Tokuyama et al., 1982). With continued wheel access, feeding, however, eventually recovers to consumption levels comparable to, or higher than, that of sedentary rats (Levitsky, 1970; Mueller et al., 1997; Tokuyama et al., 1982). For example, Levitsky (1970) found that food intake was severely depressed for active animals during the first 4-6 days of wheel access; however, by 15 days of wheel access, the active and sedentary groups did not differ in food intake.

Not surprising, with activity increasing and food intake initially being suppressed, animals come to weigh less than sedentary control rats. In males, which are gaining weight, this usually means they show a slower rate of weight gain. Looy and Eikelboom (1989) found that in male rats, weight initially decreased with wheel access and was maintained at a reduced percentage of sedentary control rats. Other studies have shown that this weight reduction (relative to home cage controls) is maintained for as long as animals have wheel access (Collier, 1970; Cortright et al., 1997; Goodrick, 1980). Thus, while the feeding suppression seems to recover after a period, the weight difference is maintained for as long as the rats have wheel access. Experiment 1 was performed to replicate the findings of suppressed feeding and weight with ad-lib wheel access, and served as the comparison for the effect of wheel access in females and weanlings.

Wheel Running, Feeding, and Weight in Adult Females

Most studies involving the investigation of food intake, exercise, and body weight have been done with adult male rats. Compared to males, behaviourial and physiological changes in females with wheel access are not well documented. Thus, Experiment 2 investigates female rats' response to wheel access on feeding and weight behaviour and then compares them to males from Experiment 1.

Females consistently demonstrate higher wheel running activity than males -- approximately, 10,000 vs. 5000 wheel turns a day, respectively (Cortright et al., 1997; Eikelboom & Mills, 1988; Lambert & Kinsley, 1983; Richter, 1927; Slonaker, 1908; Tokuyama et al., 1982; Wang, 1923). Richter (1927) even reported a female rat running 47 km in a 24 hour span! Some researchers (e.g., Beatty, 1979; Lambert & Kinsley , 1983) suggest that the sex differences in running wheel activity are strongly influenced by activational effects of female hormones. Specifically, estrogen has been found to be the activity-promoting hormone in females (Roy & Wade, 1975). For example, Stern and Zwick (1972) found a 15-34% suppression in wheel activity when female rats were ovariectomized. Looy (1986) found that ovariectomized rats ran an amount similar to that seen in males. With estrodial benzoate replacement injections in ovariectomized females, wheel activity is stimulated (Gentry & Wade, 1976; Looy, 1986). Further evidence for activational effects may be inferred by the observation that female running shows periodicity that parallels the oestrous cycle (Anantharaman-Barr & Decombaz, 1987).

Sex differences also exist in rat food intake and body weight, even in the absence of wheel access. Males eat and weigh more than females (Applegate et al., 1982; Goodrick, 1980; Hill et al., 1984; Leibowitz, Lucas, Leibowitz, & Jhanwar, 1991; Slonaker, 1908). Adult male rats continue to gain weight for most of their lives (sometimes reaching weights of 600+ grams). Females, however, stop gaining weight at about 250-350 grams and maintain this weight for most of their lives. Weight regulation seems to be affected by gonadal hormones (Wade & Gray, 1979). Females that are ovariectomized gain weight like males and estrogen replacement suppresses this weight gain (Looy, 1986). Thus, the difference in body weight also seems to be a function of estrogen. Because of these preexisting sex differences, it was possible that the effects of wheel exposure would impact feeding and weight differently in males and females.

While forced (Applegate et al., 1982; Eugene et al., 1969; Katch et al., 1979; Nance et al., 1977) and voluntary exercise (Levitsky, 1970; Looy & Eikelboom, 1989) initially suppresses feeding in males, the picture is not as clear for females. With both forced and voluntary exercise in females, some studies find an initial feeding suppression; (Premack & Premack, 1963; Tokuyama et al., 1982), while others find no feeding change or an immediate elevation (Mayer, Marshall, Vitale, Christensen, & Stare, 1954; Nance et al., 1977; Scheurink, Ammar, Benthem, Dijk, and Sodersten, 1999). The effects of exercise on body weight show a similar inconsistency. Some researchers find an exercise induced weight reduction, others do not.

Forced exercise in females most often results in no suppression of feeding. Nance et al.(1977) and Applegate et al. (1982) found males, but not females, show a feeding suppression with forced treadmill running. The females showed an increase in food intake sufficient to maintain their body weight at controls' levels. Mayer et al. (1954) found elevations in the feeding of females with exercise durations (forced exercise) of more than an hour day. If the exercise sessions were less than one hour in length the feeding was suppressed relative to sedentary control females. In their study, all the groups forced to exercise showed a weight suppression relative to sedentary animals.

A similar inconsistent picture emerges when the effects of voluntary exercise on feeding in females are explored. Some studies report that with initial wheel access females show a feeding suppression that recovers over several days (Jones et al., 1990; Premack & Premack, 1963; Tokoyama et al., 1982). Tokoyama et al. (1982) and Goodrick (1980) found that with wheel introduction both males and females regulated their weight at a lower level than the sedentary controls. In contrast, Scheurink et al. (1999), Cortright et al. (1997) and Pitts (1984) report wheel access does not suppress feeding in females and, in fact, Scheurink et al. (1999) document an almost immediate 130% elevation in feeding with wheel access. Anantharaman-Barr and Decombaz (1987) also found that females with wheel access demonstrate hyperphagia. As wheel access did not suppress food intake in these four studies, it also did not affect body weight. Cortright et al. (1997) report that despite the wheel induced hyperphagia and maintenance of body weight, both males and females are in an estimated negative energy balance relative to sedentary animals. The researchers suggested that females, because they maintain their weight, are somehow better protected against weight loss.

Thus, while for males exercise seems to reliably produce a feeding and weight suppression, the effects are more variable in females. In studies on the effect of wheel running on females there are considerable differences in the ages of the animals, frequency of data collection, specifics of the wheel access, and exercise procedure used, all of which might produce the differences observed. Given this variability, further exploration comparing females to males using consistent procedures are necessary. Thus, Experiment 2 investigated female rats' response to wheel access on feeding and weight behaviour and then compared them to adult males from Experiment 1.

Wheel Running, Feeding, and Weight in Weanling Males

As indicated above, studies in females on the effects of wheel access on feeding and weight are inconsistent. One variable that may be responsible for the differences is the age at which the rats are tested. In studies with older (50+ days old) rats, Jones et al. (1990), Premack & Premack (1963), and Tokoyama et al. (1982) find a feeding suppression, and Goodrick (1980) and Tokuyama et al. (1997) find that wheel access resulted in a lower level of weight regulation for females. Scheurink et al. (1999) reports an immediate elevation in feeding with exercise in what appeared to be older female rats (age was not reported, only weight); however, this study did not report many details on the exercise protocol or other methods. In studies with younger (21 days old) rats, Anantharaman-Barr and Decombaz (1987) and Cortright et al. (1997) found that females with wheel access initially ate more food, and Pitts (1984) reports no effect of wheel access on feeding. Cortright et al. (1997) and Pitts (1984) found females with wheel access did not differ in weight from their sedentary control. These differences suggest that age may play a role in the inconsistent findings in females of the dimorphic responses to feeding and weight induced by wheel running. To determine if age alone has an impact on the wheel running effects, Experiment 3 investigated weanling male rats' response to wheel access on feeding and weight comparing them to the adult males from Experiment 1.

The nature and/or extent of the responses to wheel introduction could depend on the age (or rapid weight gain) of the rats. Most investigations do not directly compare how the age at which the animal is introduced to a wheel impacts feeding and weight regulation. Many studies start their experiments with animals approximately seven weeks of age (Goodrick, 1980; Holloszy, 1997; Holloszy, Smith, Vining, & Adams, 1985; Lambert & Kinsley, 1983; Levitsky, 1970; McMillan, McClure, & Hardwick, 1995; Mondon et al., 1985; Peng, Jiang, & Hsu, 1980; Peng & Kang, 1984; Rolls & Rowe, 1979; Tokuyama et al., 1982). Only Cortright et al. (1997) and Pitts (1984) have used young, weanling, rats in their study and only Pitt (1984) briefly compared females introduced, at several ages, to the wheel. Unfortunately the initial effects of wheel access at the different ages were not reported, as the emphasis in this study was on body composition.

When a wheel is introduced to weanlings (animals younger than 35 days), a steep increase in running is observed over the period from 25 to 50 days of age (Cortright et al., 1997; Pitts, 1984). The maximal running plateau persists from 50 until about 75 days after which it subsides (Pitts, 1984). Others have reported that the running begins to decrease around 18 weeks (Dawson & Crowne, 1987; Goodrick, 1980; Mondon et al., 1985). The activity in a wheel appears to be a quadratic trend–running increases in the first period of life, then begins to decrease drastically in old age (Dawson & Crowne, 1987). Furthermore this trend is consistent for both males and females (Goodrick, 1980; Rolls & Rowe, 1979). When a wheel is introduced to adult animals, a similar increase in running is seen over days (Looy & Eikelboom 1989; Mueller et al., 1997). This increase has been suggested to be a function of the physical ability of the rats to run (Mueller, Herman, & Eikelboom, 1999). Thus it is not clear if the initial running increase in weanlings is any different from that which is seen in adult animals. Looy and Eikelboom (1989) report that animals introduced to the wheel later in the experiment (being older and heavier) do not show the same increase over days that are seen in younger adult animals. Direct comparison of wheel introduction at various ages using consistent procedures is necessary to see if the pattern of running changes with age.

The feeding behaviour of weanling rats has not been extensively studied. Rat pups are born immature. Thus, they cannot seek food. Their only source of food early in life comes from their mother and as animals mature, they start to eat independently. In a laboratory setting, the mother is usually taken away at 21 days – a period known as weaning. The animals then have to find food for themselves. Food intake increases steadily as animals get older. Leibowitz et al. (1991) showed that males increased consumption from about 40 kcal on day 21 to about 95 kcal by day 49 and 120 kcal by day 70. Thus, over this age period, a rat increases its food consumption and gains weight rapidly. The amount of food consumed increases for about 11 weeks, and then plateaus until 16 weeks of age (Peng et al., 1980). At this time feeding begins to slowly decrease over the next year.

As with food intake, body weight increases steadily as a function of age (Leibowitz et al., 1991; Pitts, 1984). Leibowitz et al. (1991) revealed a weight change of 2 grams/day for males prior to weaning (21 days old). After weaning, weight gain increased with the greatest daily increase in weight starting around day 28 (about 10 grams/day) and lasting until puberty (day 48) (Leibowitz et al., 1991; Pitts 1984). After this peak weight gain period, these rats exhibited a smaller daily body weight gain (about 5 grams/day) until the end of the experiment (day 77).

As weight gain is rapid immediately after weaning, it might be expected that wheel introduction at this age would have different effects on feeding than if wheel introduction occurs at an age when weight gain is slower (e.g., adulthood). The question is: What happens when a wheel is introduced to an animal during a time when food intake is maximal and weight gain rapid? Thus, for the last experiment, a wheel was introduced to males during their peak weight gain period to see if this changed any of the feeding or weight regulatory behaviours. Wheel introduction early in life may affect weight less than does wheel introduction later in life, as suggested from the female data (Cortright et al., 1997; Pitts, 1984).

Previous Methodology

The methodologies of previous investigations of feeding and weight regulation as a function of wheel running have involved relatively coarse measurements of wheel running, food consumption, and body weight. For example, Tokuyama et al. (1982) measured feeding and wheel activity daily, and weight every fifth day. Their data were presented as 10 day means. Cortright et al. (1997) measured total feeding over two days a week, wheel activity daily, and weight every second day. Their data were presented as weekly means. Goodrick (1980) measured weight weekly until 6 months of age, after which the rats were weighed monthly. Given these global measures, it is difficult to determine accurately how wheel access modifies these various measures. Some inconsistencies in the literature may be due to the coarse nature of the measures.

The present series of experiments was designed to replicate previous findings of feeding suppression with initial wheel access and explore wheel running, food intake, and body weight in adult male rats using smaller units of time. The methodology incorporated in this study follows a paradigm frequently used in our lab: feeding and wheel running was reported as nightly means and body weight was reported daily. Most studies (e..g, Cortright et al., 1997) report their means based on weekly data. Because of equipment availability, only a limited number of animals could be studied at any time. Thus all experiments were run in multiple replications. All cages and wheels were housed in a single room to permit interfacing to the computer. However, it was felt that different groups should not be housed together. It was feared that the presence of the other gender might influence the animals and change the running behaviour. Males, for example, might be likely to run more on a night there was an estrous female in the room. In each replication, four of the chambers had a wheel available and either three or four chambers did not. This made it possible to compare groups with and without wheel access.

Experiment 1 was designed to provide more information of how these behaviours changed and interacted after a wheel was introduced to adult male rats. Experiment 2 investigated if the results from Experiment 1 generalized to adult females. Experiment 3 investigated if the results of Experiment 1 generalized to younger males.

For each experiment the replications were combined and wheel access animals were compared to animals without wheels. As adult males have been studied most frequently, these animals provided a standard to which other experiments (2 and 3) could be compared. Thus, females and young males, with and without wheel access, were first compared separately. Then each was compared to the adult males to see if the effects of the wheel access were similar first in adult males and females and second in adult and young males.

Experiment 1

Experiment 1 was designed to replicate previous findings of feeding suppression with initial wheel access (Applegate et al., 1982; Cortright et al., 1997; Eugene et al., 1969; Katch et al., 1979; Nance et al., 1977; Levitsky, 1970; Looy & Eikelboom, 1989; Pitts, 1984) and explore wheel running, food intake and body weight in **adult male** rats using more frequent measurements of behaviour. Adult male rats were first permitted to habituate to our experimental housing conditions. Then, wheels were made available to half the animals to see how feeding and weight changed.

Methods

Animals. Adult male (n = 15) Sprague-Dawley rats (Charles River, Canada) were housed individually, and maintained on a 12:12 L/D cycle, with lights on at 06:30 h. Rats weighed 306-360 g (64 days old) at the time of wheel introduction. All animals had ad lib access to Bio-Serv 45 mg grain based food pellets and tap water.

Apparatus. Eight cages (25 X 30 X 25 cm), four with attached custom built running wheels (11 cm wide, 33 cm in diameter) were used. The cages were placed on tables side by side preventing rats from seeing one another; however, they could hear and smell one another.

Data Collection. All data collection occurred in the animals' colony room. The feeding apparatus, a modified version of the system described by West, Tengan, Smith and Samson (1983), recorded the number of pellets taken out of the Coulbourn feeding cups. When the animal removed a pellet, the system immediately replaced the pellet from the Colbourn feeder. The cage floor consisted of equally spaced grid bars, which permitted a pellet to drop onto a waste tray if the rat did not eat it. The uneaten pellets were counted daily and were not further analyzed as they were always less than 1% of total daily consumption. The number of wheel revolutions was recorded using magnetic reed switches. Both feeding and wheel turns counting systems were interfaced with a Mini-Mitter Co.Vital View data collection system run under Windows 95. Data were collected every 5 seconds for feeding and wheel turns. Weight was recorded daily.

Procedure. Following arrival in the laboratory, the animals were habituated in standard hanging cages for several days to the colony and the weighing procedure. After this habituation period, animals were moved into the experimental cages and the data collection for feeding, and weight began. Wheel running was prevented by a plate blocking wheel access for 14 days. The last 5 days were the baseline period used for data analysis. The plates, which blocked wheel access, were then removed permitting running for the experimental group (WH, n = 8). The control group (NW, n = 7) did not have wheels attached to their cages.

The data collection for feeding and wheel turns was continued for 32 days, at 5 second resolutions and combined into nightly totals, while weight was measured once daily. Animals were only disturbed during the study once daily when they were weighed, and feeders were cleaned. This occurred at about 9:00 a.m. daily, during the light phase of the experiment. The bedding was changed early morning (7:00 a.m.) every fourth day during the study. Because of equipment limitations, the data were collected in 2 replications.

Since Richter's (1927) work, it has been known that in rats activity (e.g., feeding and physical activity) occurs largely at night. As rats are nocturnal, analysis was performed on food consumption and wheel running for the 12 hours of the dark phase.

The length of this experiment resulted in some data collection errors due to power outages and equipment failure. For Days 16-21 of the first replication, data was lost for wheel turns (n = 4) and pellet consumption (n = 7) due to computer failure. As this was a data storage problem, rats continued to have full access to the food pellets and the wheel (if in the WH group) throughout this period. Although no data analysis was performed for these days, data points for Days 16-21 on Figures 1 and 2 were based on means from the second replication only.

Results and Discussion

The analysis was performed on feeding and weight separately for five day blocks of: (a) before wheel access, baseline (BASE); (b) initial wheel access, days 1-5 (D1-5), days 6-10 (D6-10), and days 11-15 (D11-15); and (c) late wheel access, days 28-32 (D28-32).

Wheel Turns. From Figure 1, it can be seen that animals with wheel access increased their night time running for about the first three weeks of wheel access and then running reached a plateau.

Wheel running (12 hours of dark phase) was explored in a repeated measures analysis of variance (ANOVA) to see if the averages of the four blocks of five days (D1-5, D6-10, D11-15, D28-32) were different.

The four block repeated measures ANOVA, revealed that there was a wheel running difference among the four blocks of days, $\underline{F}\ (3, 21) = 16.99$, $\underline{p} < .001$. Pairwise T-tests (using a Bonferroni correction), further confirmed that running increased from: D1-5 to D 6-10, $\underline{t}\ (7) = -3.64$, $\underline{p} < .05$, and D6-10 to D28-32, $\underline{t}\ (7) = -2.95$, $\underline{p} < .05$. Thus, running was still increasing from D6-10 to the end of the experiment.

The last two blocks of five days were also analyzed to confirm that running had reached a plateau. A pairwise T-test was performed on the average running of D24-27and D28-32. The analysis showed that the running from the block of D24-27 was not different from D28-32, ($\underline{t} < 1$). Thus the WH group had apparently reached a running plateau, as can be seen in Figure 1.

Food Intake. Figure 2, shows that food consumption during BASE period in the two groups of rats did not differ; however, with initial wheel access the WH group animals showed a marked feeding suppression that recovered after several days. Because wheel access has different effects on feeding at different periods, the averages of the blocks were **not** compared as in the wheel running analysis. The days within the blocks were analyzed to see if the groups consumed in the same manner over the days of the individual blocks. Thus, Group X Days repeated measures ANOVAs were conducted for 12 hours of dark phase food intake for adult males, in WH and NW groups, over days for each of the five blocks separately.

At BASE, the Group X Days ANOVA for feeding revealed that the two groups of rats did not show any differences in food consumption and that there was no feeding change over days, suggesting food consumption was stable. For D1-5, there was a significant Group effect, $F(1, 13) = 29.70$, $p < .001$, and Groups X Days interaction, $F(4, 52) = 2.55$, $p = .05$. When the groups were analyzed separately, the Days ANOVA revealed a significant Days effect only for the WH rats, $F(4, 24) = 3.48$, $p = .02$. The two groups were analyzed for each day separately. The pairwise comparisons (using Bonferroni correction) revealed that the NW rats ate more than the WH rats on days 2 through 5: $t(13) = 4.34$, $p = .001$, $t(13) = 4.28$, $p = .001$, $t(13) = 3.68$, $p = .003$, and $t(13) = 3.91$, $p = .002$, respectively (see Figure 2). This feeding suppression was not evident on the first day, suggesting the suppression was not an immediate effect.

For D6-10, D11-15, and D28-32 the Group X Days ANOVA for feeding revealed no significant effects. Thus, both the animals in the WH and NW groups were consuming a similar number of pellets by D6-10.

In adult males with initial wheel access, a feeding suppression was seen. Food consumption recovered a few days later and no significant differences were seen after the recovery between WH and NW rats. Figure 2 suggests that by Day 24 until the end of the experiment the WH group rats were consuming more pellets than the NW group rats; however, this result was not significant; D28-32, $F(1, 13) = 1.38$, $p = .26$. Thus we must conclude that all animals were consuming a similar number of pellets at the end of the experiment. It is possible that if the group size was increased or if the experiment was continued longer the feeding difference might have occurred. Other studies have demonstrated a significant increase in feeding when wheel access was continued for an extended period (Mueller et al., 1997; Tokoyama et al., 1982).

Weight. Figure 3 shows that animals in the NW group gained weight throughout the experiment, but the WH group rats did not gain weight with initial wheel access. It appears that once the wheel was available, the WH group rats regulated their weight at a lower level than the NW group rats for the duration of the experiment.

Because wheel access has different effects on weight at different periods, the averages of the blocks were **not** compared as in the wheel running analysis. The days within the blocks were analyzed to see if the groups regulated weight in a similar manner over the days of the individual blocks. Group X Days repeated measures ANOVAs were conducted for daily body weight for adult males, in WH and NW groups, over days for each of the five blocks separately.

The Group X Days ANOVA of the weight of the adult males during BASE showed a Days effect, F (4, 52) = 199.96, p < .001. Figure 3, shows that all animals gained weight over baseline days and the groups did not differ significantly at this time.

For D1-5, a similar Group X Days ANOVA of weight gain revealed both a significant a Days effect, F (4, 52) = 25.59, p <. 001, and a Groups X Days interaction, F (4, 52) =11.03, p <. 01. When the groups were analyzed separately, the Days ANOVA revealed only a significant Days effect for the NW rats, F (4, 24) = 116.15, p < .001. Figure 3 shows that the WH group rats maintained their weight and the NW rats continued to gain weight over days 1 to 5. When the two groups were analyzed for each day separately, the groups did not differed on any of the days 1 through 5. So while the rate of weight gain was different in the two groups it did not result in a significant group difference over these days.

The Group X Days ANOVA for D6-10 revealed a significant Days effect, F (4, 52) = 96.48, p <.001 and a Group effect that approached significance, F (1, 13) = 3.92, p = .07. For D11-15 and D28-32 there was a significant Days effect, F (4, 52) = 12.12, p < .001 and F (4, 52) = 30.40, p < .001, respectively; and a Group effect, F (1, 13) = 4.85, p < .05 and F (1, 13) = 4.58, p = .05, respectively. All animals gained weight, but from Figure 3 the WH group gained weight slower and gradually over days 6 to 15 came to weigh significantly less than the NW group rats.

The results from Experiment 1 demonstrate that running increased to a plateau over 21 days, feeding initially decreased but returned to baseline levels, and weight was decreased in wheel rats (relative to rats without wheel access) from when the wheels were made available to the end of the experiment. These results are consistent with previous work (Applegate et al., 1982; Cortright et al., 1997; Eugene et al., 1969; Katch et al., 1979; Levitsky, 1970; Looy & Eikelboom, 1989; Mueller et al., 1997; Nance et al., 1977; Pitts, 1984) and provided a baseline for the subsequent studies with females and weanlings where the same procedure was used.

Experiment 2

Males and females differ in weight, food consumption, and wheel running. This difference, as discussed earlier, is probably a function of gonadal hormones (Beatty, 1979; Lambert & Kinsley , 1983). Literature on the effects of exercise is inconsistent for females (Cortright et al., 1997; Nance et al., 1977; Pitts, 1984; Premack & Premack, 1963; Tokuyama et al., 1982). Thus, this experiment is a replication of the first experiment with **adult females.** Because this experiment was designed to see if females show the same initial feeding and weight suppression that is seen in adult males, only a limited number of days of wheel access were needed. After the effects of wheel access in females were studied, the two groups of females were compared to the males from Experiment 1.

Methods

Animals. Adult female (n = 13) Sprague-Dawley rats (Charles River, Canada) weighed 242-298 g (64 days old) upon wheel introduction.

Procedure. The apparatus, procedure, and methods of data collection were the same as in Experiment 1. After 14 days of no wheel access (the last 5 days of which served as baseline), 8 animals (WH) were given 15 days of wheel access and the remaining 5 rats served as controls (NW). Wheel turns, food intake, and body weights were recorded as in Experiment 1. Because of equipment limitations, the data was collected in 2 replications.

A 20 min power failure was experienced on Day 8 of the first replication, thus wheel turn data (n = 4) and pellet consumption data (n = 8) for this night was not recorded, but except for the time of the power failure animals had access to food and wheel (if in WH group). No data was collected for the rest of that night because of a programming failure. An average from day 7 and day 9 for wheel turns and pellet consumption was recorded for those animals that did not have data recorded for day 8 and the degrees of freedom of the ANOVAs were adjusted as appropriate.

Results and Discussion

As in Experiment 1, the initial within experiment analysis were performed on feeding and weight separately for five day blocks of: before wheel access, baseline (BASE); and for the period of, days 1-5 (D1-5), days 6-10 (D6-10), and days 11-15 (D11-15).

Wheel Turns. Figure 4 shows that running increased to day 10. Wheel running in WH group females (12 hours of dark phase) was explored in a repeated measures ANOVA to see if the averages of the three blocks of five days (D1-5, D6-10, D11-15) were different. The repeated measures ANOVA of running revealed that running increased over the three blocks of days, F (2, 14) = 21.36, p < .001. The Bonferroni corrected T-test pairwise comparisons further confirmed that running increased from D1-5 to D6-10, t (7)= -5.60, p = .01.

Figure 5 combines the wheel running data for the males from Figure 1 with that of females from Figure 4 and shows that females run initially as much as males, but after about 6 days of wheel access the females began to run more than the males. Sex differences in wheel running (12 hours of dark phase) were explored by comparing running in males from the first experiment with the females in this experiment in three Sex X Days repeated measures ANOVAs to see if over days in any given block of five days (D1-5, D6-10, D11-15) the sexes differed. The Sex X Days ANOVA of running revealed that on D1-5 a significant main effect of Days, *F* (4, 56) = 17.19, *p* < .001. Thus the sexes both increased their running and did not differ in the amount run over D1-D5. D6-10, there was a main effect of Days, *F* (4, 52) = 5.41, *p* = .01 (df correction), and a trend in the main effect of Sex, *F* (1, 14) = 3.32, *p* = .09. The females began to run more than the males, with both sexes increasing their running over days. On days D11-15, there was a Days effect, *F* (4, 56) = 3.39, *p* = .02 and Sex X Days interaction, *F* (4, 56) = 3.64, *p* = .01. As seen in Figure 5, the females continued to increase their running over theses days. Males seemed to have reached a stable level of daily running over these days. When the sexes were analyzed separately in a Days ANOVA, there was only a significant Days effect for females, *F* (4, 28) = 4.67, *p* = .005.

These results are similar to what has been previously reported females run more than males. For females, the running had not reached a plateau during the 15 days of wheel access. Previous research has found that after about 21 days of wheel access, a plateau level of running can be reached (Anantharaman-Barr & Decombaz, 1987; Cortright et al., 1997; Eikelboom & Mills, 1988; Mondon et al., 1985; Pitts, 1984). In Experiment 1, the males reached a running plateau at about two weeks of wheel access.

However, Experiment 2 only investigated initial wheel access for female rats, thus given more days of wheel access, females would most likely reach a running plateau later. The sex difference in running (females running more than males) is consistent with previous findings (Cortright et al., 1997; Eikelboom & Mills, 1988, Lambert & Kinsley, 1983; Richter, 1927; Slonaker, 1908).

Feeding. Focusing only on females again, Figure 6 shows that during BASE, feeding in the two groups of female rats did not differ; however, with initial wheel access the WH group rats showed a feeding suppression that recovered after several days.

Because wheel access has different effects on feeding at different periods, the averages of the blocks were **not** compared as in the wheel running analysis. The days within the blocks were analyzed to see if the female groups were eating in the same manner over the days of the individual blocks. Thus, Group X Days repeated measures ANOVAs were conducted for 12 hours of dark phase food intake for adult females, in the WH and NW groups over days for each of the four (BASE, D1-5, D6-10, D11-15) blocks.

During BASE, the Group X Days ANOVA of feeding revealed no significant differences. Thus, before wheel introduction, food consumption in the two groups did not differ. For D1-5, the Group X Days ANOVA revealed only a Group effect, $\underline{F}$ (1, 11) = 9.59, $\underline{p} = .01$. From Figure 6, the WH group rats displayed a feeding suppression, consuming fewer pellets than the NW group rats. By D6-10, the Group effect had disappeared, there were no significant effects for the blocks of days D6-10 and D11-15. From day 6 to the end of the experiment, both WH and NW group females were consuming a similar number of pellets.

Figure 7 combines the feeding data for the males from Figure 2 with that of females from Figure 6 and shows that: (a) males ate more than females; (b) both WH group animals showed a suppressed food intake with initial wheel access that recovered after several days of wheel access; and, (c) for both the males and females, after several days of wheel running, feeding does not differ in the WH and NW groups.

Sex X Group X Days repeated measures ANOVAs were conducted for 12 hours of dark phase food intake for females and males, in WH and NW groups, over days for each block of five days (D1-5, D6-10, D11-15). The Sex X Group X Days ANOVA for feeding found for D1-5 there was a significant Sex effect, $\underline{F}$ (1, 24) = 25.77, $\underline{p} < .001$, Group effect, $\underline{F}$ (1, 24) = 31.65, $\underline{p} < .001$, and Group X Days interaction, $\underline{F}$ (4, 96) = 4.29, $\underline{p} = .003$. As there were no interactions involving the sex, the WH and NW groups could be collapsed on sex. The groups were analyzed separately, the Days ANOVA revealed that there was a Days effect for the WH rats, $\underline{F}$ (4, 60) = 3.72, $\underline{p} = .009$. NW rats seemed to be consuming a stable amount over these days. When WH and NW group rats (collapsed on sex) were compared on each individual day (days 1 through 5), the pairwise T-test (using the Bonferroni correction) revealed that on days 2, 3, 4 and 5 the groups differed, $\underline{t}$ (26) = 4.50, $p < .05$, $\underline{t}$ (26) = 5.16, $\underline{p} < .05$, $\underline{t}$ (26) = 3.94, $p < .05$, and $\underline{t}$ (26) = 3.10, $\underline{p} < .05$, respectively. The WH males and females ate less than their respective controls. At the day of maximum suppression WH males (day 3) ate 38% less than their NW controls and WH females (day 4) ate 47% less than their controls.

The Sex X Group X Days ANOVA of feeding revealed that for D6-10 and D11-15, there were only significant Sex effects, $\underline{F}$ (1, 24) = 46.44, $\underline{p} < .001$ and $\underline{F}$ (1, 24) =

18.09, p < .001, respectively. The males ate more than the females (see Figure 7).

The male rat has previously been reported to eat more than the female rat (Applegate et al., 1982; Goodrick, 1980; Hill et al., 1984; Leibowitz et al., 1991), thus our finding that the males eat more than females, was not surprising. The initial feeding suppression with the introduction of the wheel in female rats has not been as well documented. In this experiment, females with wheel access experienced the feeding suppression. The magnitude of the suppression was similar to the magnitude found in the suppression of the WH males (Experiment 1). In addition the initial feeding suppression recovered over several days of wheel access for both males and females.

Weight. Focusing only on females again, Figure 8 shows that animals in the NW group very slowly gained weight throughout the experiment. The WH group rats did not gain weight throughout the experiment. Thus, the weight difference between the groups was becoming larger.

Because wheel access has different effects on weight at different periods, the averages of the blocks were **not** compared as in the wheel running analysis. The days within the blocks were analyzed to see if the groups regulated weight in the same manner over the days of the individual blocks. Thus, Group X Days repeated measures ANOVAs were conducted for daily body weight for adult females, in the WH and NW groups over days for each of the four blocks.

The Group X Days ANOVA of adult female weight gain revealed that during BASE there was a Days effect, F (4, 44) = 18.22, p < .001. From Figure 8, it was observed that all animals gained weight over baseline days. For D1-5, there was only a significant Groups X Days interaction, F (4, 44) = 5.18, p < .05. When the groups were analyzed separately in a Days ANOVA, the Days ANOVA revealed a Days effect for WH and NW rats, F (4, 28) = 3.32, p = .02 and F (4, 28) = 5.56, p = .005, respectively. Figure 8 suggests that for the NW group rats the Days effect is due to their continuing weight gain over D1-5, whereas the WH group rats they seem to lose weight. When the 1 through 5 were analyzed separately, comparing WH and NW females, the pairwise T-test (using the Bonferroni correction) revealed no significant difference between WH and NW rats on any of the days in this block.

For the Group X Days ANOVA for D6-10, there was a significant Days effect F (4, 44) = 7.44, p < .001 and a Group X Days interaction, F (4, 44) = 3.05, p < .05. When the groups were analyzed separately, the Days ANOVA revealed only a days effect for the NW rats, F (4, 28) = 13.51, p < .001, suggesting they continued to gain weight. When the days 6 through 10 were analyzed separately, the pairwise T-test (using the Bonferroni correction) revealed no significant differences between WH and NW rats on any of the days in this block. For D11-15, there was a Group effect, F (1, 11) = 4.90, p < .05, and a Days effect, F (4, 44) = 3.29, p < .05. From Figure 8, it can be seen that the WH group rats weighed less than the NW group rats, but this difference only becomes significant later in the experiment (D11-15).

Figure 9 combines the weight data for the males from Figure 3 with that of females from Figure 8 and shows that: males weighed more than the females, and the WH groups for each sex gradually regulated weight at a lower level than the appropriate control NW group animals. Sex X Group X Days repeated measures ANOVAs were conducted for daily body weight for females and males, in WH and NW groups, over days for each block of five days (D1-5, D6-10, D11-15). Because of the complexity of the design, the results from the Sex X Group X Days ANOVAs for the weight data in this section are summarized in Table 1 for male and female rats with and without wheel access over D1-5, D6-10, and D11-15.

The Sex X Group X Days ANOVA for D1-5 revealed a significant: Sex effect, F (1, 24) = 103.97, p < .001; Days effect, F (4, 96) = 6.96, p = .004 (with the Greenhouse-Geisser correction for sphericity); Sex X Days interaction, F (4, 96) = 12.77, p < .001; and Group X Days interaction, F (4, 96) = 14.58, p < .001.

The Sex X Groups X Days ANOVA for D6-10 revealed a significant: Sex effect, F (1, 24) = 146.72, p < .001; Group effect, F (1, 24) = 6.25, p = .02; Days effect, F (4, 96) = 53.63, p < .001; Sex X Days interaction, F (4, 96) = 25.09, p < .001; and Group X Days interaction, F (4, 96) = 2.57, p = .04.

The Sex X Groups X Days ANOVA for D11-15, revealed a significant: Sex effect, F (1, 24) = 165.93, p < .001; Group effect, F (1, 24) = 9.85, p = .004; Days effect, F (4, 96) = 13.30, p < .001; and, Sex X Days interaction, F (4, 96) = 4.05, p = .004.

Overall animals gained weight over these experiments (Days effects), but this must be qualified for some conditions. Males weighed more than females (Sex effects) and female average weight gain over the experiment is less than that of males (Sex X Days interactions). The wheel effect on weight is gradual, resulting in a Group X Days interaction for D1-5 and D6-10, but by D11-15 the wheel effect was well established and so there was a significant Group effect. However, there never was a significant Sex X

Group or Sex X Group X Days interaction suggesting the effects of wheel access on weight were similar in males and females.

Adult male and female rats given wheel access initially stopped gaining weight (males) or lost weight (females) and continued to regulate their weight at a lower level than the rats given no wheel access. However the female rats did not gain weight as rapidly as the male rats. This may be related to the sexual dimorphism in growth pattern in the rat (Kennedy, 1969; Prats, Monfar, Castella, Iglesias & Alemany, 1989). Males grow throughout adult life, and females reach an asymptotic weight. As can be seen in Figure 9, female NW rats gained weight very slowly in comparison to both the male WH and NW rats, suggesting the female NW rats were approaching their asymptotic weight. This may account for the finding that the female WH rats no longer gained weight as did the female NW rats. Perhaps the female WH rats had reached their maximum weight. Wheel access may lower the asymptotic weight of females.

Experiment 3

The findings in Experiment 2 were consistent with studies that have used adult female rats (Goodrick, 1980; Tokuyama et al., 1997). Most studies reporting no weight change with wheel access employ very young females. During the period of rapid growth wheel access may differently affect feeding and weight gain. Experiment 3 was designed to explore in more detail what happens to feeding and weight regulation when a wheel was introduced at a time when food consumption is great and weight gain is rapid. Peak weight gain for male rats is from days 28-49 and then it starts to decline (Leibowitz et al., 1991). Most of the studies of wheel access employed older, heavier males for when weight gain is lower. Studying feeding and running in weanlings will help determine if the suppression is seen in younger animals when weight gain is rapid. Thus, younger males would be compared to older males to provide information on whether or not age plays a role in these wheel running effects. Thus, Experiment 3 employed **male weanlings** in the same paradigm as Experiment 1. More days of wheel access were allowed for these animals because the initial effects of wheel access on weight gain were not as pronounced.

Methods

Animals. Male (n = 21) Sprague-Dawley rats (Charles River, Canada) weighed 50-60g (30 days) upon wheel introduction.

Procedure. The apparatus and methods of data collection were similar to Experiment 1. After 7 days of baseline, 12 animals (WH) were given 48 days of wheel access. The remaining 9 animals served as controls (NW). Wheel turns, food intake, and body weight were recorded as in Experiment 1. Because of equipment limitations, the data was collected in 3 replications.

During the baseline period of replication 1, there was a data collection problem, thus pellet consumption data was lost for animals (NW, n = 3; WH, n = 4). No data was lost for wheel running, because during baseline, wheels were locked.

Results and Discussion

The analysis was performed on feeding and weight separately for five day blocks of: (a) before wheel access, baseline (BASE); (b) initial wheel access, days 1-5 (D1-5), days 6-10 (D6-10), and days11-15 (D11-15) of wheel access; and (c) late wheel access, days 28-32 (D28-32) and days 44-48 (D44-48).

Wheel Turns. From Figure 10, it can be seen that animals with wheel access increased their running rapidly over the first five days; however, after this period, wheel running slowly increased. It appears from Figure 10 that a plateau was reached after about two to three weeks of wheel access. Wheel running (12 hours of dark phase) was explored in a repeated measures ANOVA to see if the averages of the five blocks of five days (D1-5, D6-10, D11-15, D 28-32, D44-48) were different.

The repeated measures ANOVA, revealed that there was a wheel running difference among the five blocks, $F\ (4, 44) = 5.43$, $p < .001$. The Bonferroni corrected pairwise T-test comparisons showed that running increased from the blocks: D1-5 to D6-10, $t\ (11) = -2.74$, $p < .05$, but not significantly from D6-10 to D28-32. Block D28-32 did not differ from the block D44-48 ($t < 1$) suggesting the WH group rats had reached a running plateau. Given the results of the pairwise tests, the plateau was reached between the blocks of D6-10 to D28-32.

Figure 11 combines the wheel running data for the adults from Figure 1 with that of weanlings from Figure 10 and shows that the weanling rats ran slightly more than the adult rats for the first five days of wheel access, but for the following days of wheel access there was no difference in the amount of running. Both ages increased their running until about two to three weeks of wheel access until a plateau was reached which was similar for both ages. Age differences (between adult and weanling male rats) in wheel running (12 hours of dark phase) were explored in four Age X Days repeated measures ANOVAs to see if over days in any given block of five days (D1-5, D6-10, D11-15, D28-32) the ages differed in the amount of wheel running performed.

The Age X Group X Days ANOVA of running revealed for D1-5, only a Days effect, F (4, 72) = 10.94, p < .001. Male adult and weanling animals increased their running over Days. Although Figure 11 suggests that the weanlings ran more than the adults, this difference was not significant, F (1, 18) = 2.37, p = .14. For D6-10, there was an Age X Days interaction, F (4, 56) = 3.33, p = .02. When the ages were analyzed separately in a Days ANOVA, the adults displayed a significant Days effect, F (4, 28) = 3.11, p = .03. Adults increased their running over days, and the weanlings appeared to be running a similar amount each day. When days 6 through 10 were analyzed separately, comparing adults to weanlings, the pairwise T-test (using the Bonferroni correction) revealed the ages did not differ on any day in the amount ran. For D11-15, and D28-32, there were no significant effects. From the analysis performed in Experiment 1 and above in this experiment, adults and weanlings both reached a running plateau at about two to three weeks.

If the size difference between weanlings and adults (100g vs. 300g, respectively) is considered, the energy expenditure for running by the two age groups is unlikely to be similar. Weanlings were probably exerting proportionally more energy to turn the wheel. Even though there may be differences in energy expenditure, it seems that weanling and adult male rats have similar running activity. This suggests that the male animals, regardless of age, share a common preferred distance of running.

Food Intake. Focusing on the weanlings, Figure 12 suggests that at the time of wheel introduction, both groups were increasing their food intake rapidly; however, about three weeks later, both groups' food consumption started to stabilize. Because wheel access has different effects on feeding at different periods, the averages of the blocks were **not** compared as in the wheel running analysis. The days within the blocks were analyzed to see if the groups were eating in the same manner over the days of the individual blocks. Thus, Group X Days repeated measures ANOVAs were conducted for 12 hours of dark phase food intake for weanling males, in the WH and NW groups.

During baseline for the first replication, no data was collected on Day 0. An average from the day before and the day after could not be used to replace the missing data, as done in other cases, because Day 0 was the day before wheel access. A Group X Days ANOVA of feeding was performed for the four days of baseline prior to Day 0. Day -4 to -1 revealed only a significant Days effect, *F* (3, 57) = 6.81, *p* = .001, reflecting the increasing consumption over days. Thus, for the baseline period, the groups did not differ.

The Group X Days repeated measures ANOVA for D1-5 feeding revealed a significant Group, *F* (1, 19) = 4.32, *p* = .05, and Days effect, *F* (4, 76) = 9.60, *p* < .001. While overall consumption was increasing over days (Days effect), animals in the WH group consumed less food than animals in the NW group. For D6-10, and D11-15 similar Group X Days ANOVA revealed only a significant Days effect, *F* (4, 76) = 5.70, *p* < .001; and, *F* (4, 76) = 6.05, *p* < .001, respectively, reflecting the increasing food consumption in both groups. For D28-32, there were no significant differences. For D44-48, there was a Days effect, *F* (4, 76) = 3.11, *p* = .02; however, when averaging across blocks of D28-32 and D44-48 and then comparing them in a T-test, no difference was found, suggesting for this period food consumption had reached a maximum. The D1-5 ANOVA and Figure 12 suggest that there was a very mild disruption in food consumption for WH rats during days 1 to 5. However, after initial days (D1-5) WH and NW rats increased their food consumption at a similar rate, with a plateau reached at about two to three weeks wheel access.

Figure 13 combines the feeding data for the adults from Figure 2 with that of weanlings from Figure 12 and shows that the weanlings ate less than the adult males until about two weeks after wheel introduction, after this time both ages consumed a similar amount. The WH weanlings did not demonstrate the pronounced feeding suppression that the adult WH males did with initial wheel access. Age X Group X Days repeated measures ANOVAs were conducted for 12 hours of dark phase food intake for adult and weanling males, in WH and NW groups, over days for each block.

The Age X Groups X Days ANOVA for feeding on D1-5, revealed a significant: Age, F (1, 32) = 129.60, p < 001, Group, F (1, 32) = 40.21, p < .001, and Days effect, F (4, 128) = 4 .79, p < .01; as well as Age X Group, F (1, 32) = 20.85, p < .001, Age X Days, F (4, 128) = 9.38, p < .001, and Group X Days interactions, F (4, 128) = 4.05, p = .01 (corrected for by the Greenhouse-Geisser). The Age X Groups X Days interaction was not significant, F (4, 28) = 1.01. Given that there was no significant triple interaction, the three 2-way interactions were analyzed independently. To analyze the Group X Days interaction further, the WH and NW groups were collapsed over age, combining the adults and weanlings data. When the days 1 through 5 were analyzed, the pairwise T-tests (using the Bonferroni correction) revealed significant feeding differences between the WH and NW groups for day 3, $t(34) = -3.62$, $p < .05$. The WH rats ate less than the NW rats on day 3 (see Figure 13). To analyze the Age X Days interaction further, the WH and NW groups were combined for both adults and weanlings, so that all the adult males could be compared to all the weanlings for each day. When the days 1 through 5 were analyzed, the pairwise T-tests (using the Bonferroni correction) revealed significant feeding differences between the ages for the of days 1 through 5, $t(34) = -11.01$, $p < .01$, $t(34) = -6.26$, $p < .01$, $t(34) = -3.48$, $p < .05$, $t(34) = -3.93$, $p < .05$, $t(34) = -6.45$, $p < .01$, respectively. Clearly adults ate more than weanlings throughout this block. To analyze the Age X Group interaction further, feeding was collapsed over days and the adults and weanlings were analyzed separately to see if the WH and NW rats differed in food consumption. The WH rats ate less than the NW rats only for the adults, $F(1, 13) = 51.34$, $p < .001$. The WH and NW adults display a much greater difference in food consumption relative to the difference in feeding between WH and NW weanlings.

In summary, weanlings ate less than adult animals but showed a larger increase over days. The wheel induced feeding suppression was not evident in weanlings when compared to adult males. For Day 3, the feeding differences between WH and NW for Experiment 1 and Experiment 3 was the greatest, 38% vs. 16% respectively.

The Age X Group X Days repeated measures ANOVA for feeding revealed for D6-10 only significant Age, $F(1, 32) = 88.04$, $p < .001$, and Days effects, $F(4, 128) = 6.99$, $p < .001$. For D11-15, there was a significant: Age, $F(1, 32) = 8.44$, $p < .001$, and Days effects, $F(4, 128) = 2.53$, $p = .04$; and an Age X Days interaction $F(4, 128) = 2.90$, p = .03. For D28-32, there were no significant differences. These analysis revealed adult males ate more than weanlings. By D11-15 the difference between adults and weanlings was disappearing and feeding levels were similar for all animals till the end of the experiment.

Weanling and adult WH males both displayed a feeding suppression when analyzed separately; however, the feeding suppression was not evident when weanlings were compared to adult males. The animals in Experiment 3 were in a stage of physical development where there was rapid weight gain and food consumption increased steadily. Perhaps the weanling cannot afford to eat less during this time of rapid growth. The weanling food consumption increased until about day 15 of wheel access, at this time feeding reached a plateau, despite the rapid weight gain observed for the whole experiment (see Figure 14). This suggests that increased weight does not always correlate closely with changes in feeding

Weight. Focusing only on the weanlings again, Figure 14 reveals that the WH and NW rats increased their weight throughout the experiment. Because wheel access has different effects on feeding at different periods, the averages of the blocks were **not** compared as in the wheel running analysis. The days within the blocks were analyzed to see if the groups regulated weight in the same manner over the days of the individual blocks. Thus, Group X Days repeated measures ANOVAs were conducted for daily body weight for weanling males, in the WH and NW groups.

The Group X Days ANOVA for weight during the BASE period revealed only a significant Days effect, F (4, 76) = 2081.84, p < .001. Weanling males during BASE showed no significant difference in weight between WH and NW group rats, but all animals gained weight over this period. The Group X Days repeated measure ANOVA for weight revealed for D1-5, significant Group, F (1, 19) = 5.14, p = .04, and Days effects, F (4, 76) = 483.70, p < .001. All animals gained weight, however, the WH group rats weighed slightly less than the NW group rats. For subsequent periods animals showed significant weight gain and the Group X Days ANOVA revealed only significant Days effect: D6-10, F (4, 76) = 441.85, p < .001; D11-15, F (4, 76) = 483.29; p < .001; and, D28-32, F (4, 76) = 94.66, p < .001; and, D44-48, F = 97.42, p < .001. Animals in both groups did not reach a plateau in weight, as evidenced in Figure 14. By D6-10 and throughout the rest of the experiment the groups were similar in weight and weight regulation.

Figure 15 combines the weight data for the adults from Figure 3 with that of weanlings from Figure 14 and shows that adult males weighed more than the weanlings for the 32 days of wheel access. For the adults, the WH males weighed less than the NW males for the full 32 days of wheel access. In contrast, the WH and NW weanlings only show a slight difference in weight during initial wheel access. Age X Group X Days repeated measures ANOVAs were conducted for daily body weight for adult and weanling males, in WH and NW groups, over days for each block. The results from the four Age X Group X Days repeated ANOVAs (D1-5, D6-10, D11-15, D28-32) for weight are summarized on Table 2.

For D1-5, the Age X Group X Days repeated measure ANOVA for weight gain revealed there was a significant: Age effect, F (1, 32) = 3857.43, p < .001; Days effect, F

(4, 128) = 221.25, p < .001; Age X Days interaction, F (4, 128) = 23.50, p < .001; Group X Days interaction, F (4, 128) = 13.39, p < .001; and, Age X Group X Days interaction, F (4, 128) = 9.58, p = .001 (corrected for by Greenhouse-Geisser). The Age X Group X Days interaction was further analyzed by comparing the WH and NW groups separately for the weanlings and the adults. For the adults, the Group X Days ANOVA of weight revealed both a significant a Days effect, F (4, 52) = 25.59, p <. 001, and a Groups X Days interaction, F (4, 52) =11.03, p<. 01. When the groups were analyzed separately for adults, the Days ANOVA revealed only a significant Days effect for the NW rats, F (4, 24) = 116.15, p < .001. Figure 3 shows that the WH group rats maintained their weight and the NW rats continued to gain weight over days 1 to 5. When the two groups were analyzed for each day separately, the groups did not differ on any of the days 1 through 5. For the weanlings, the Group X Days ANOVA of weight revealed only a significant Days effect, F (4, 76) = 438.70, p < .001. At wheel introduction, both adults and weanlings gained weight, but the weight increase was more pronounced in weanlings. Not surprising, adults weighed more than weanling rats. Wheel access has a larger effect on weight in adult animals and this difference between WH and NW rats become greater over D1-5.

The Age X Group X Days ANOVA for weight revealed for D6-10, Age, F (1, 32) = 2890.29, p < .001, Group, F (1, 32) = 6.05, p = .02, and Days effects, F (4, 128) = 434.14, p < .001; as well as an Age X Days interaction, F (4, 128) = 27.00, p < .001. The Age X Group X Days ANOVA for D11-15 revealed a significant Age, F (1, 32) = 1575.15, p < .001; Group, F (1, 32) = 4.75 p < .04, and Days effects, F (4, 128) = 123.34,

$p < .001$; and again an Age X Days interaction, F (4, 128) = 16.71 $p < .001$. The Age X Group X Days for D28-32 revealed a significant Age, F (1, 32) = 206.89, $p < .001$, Group, F (1, 32) = 4.32, $p = .05$, and Days effects, F (4, 128) = 109.79, $p < .001$; as well as an Age X Days interaction, F (4, 128) = 6.74, $p = .001$ (corrected for by Greenhouse-Geisser).

Taken together these results (summarized in Table 2), over the four blocks, are due to the expected difference in body weight between adults and weanlings, and the more rapid weight increase in the weanlings. For all blocks after the first (D1-5), there is a significant overall Group effect and no significant interaction involving the group factor. This suggests that in adults and weanlings, for these blocks, wheel access animals weighed less than the NW control rats. From Figure 15, it is apparent that these results are slightly misleading. For the weanlings, there is a small difference in the weight of the WH group rats initially (for about the first 15 days). At the end of the Experiment 3, the groups start to differ, with WH rats showing a slight (though non-significant) suppression. In adults the difference is more pronounced and sustained over the entire 32 days. In weanlings, the unanalyzed period for days 16-27 the weight of the two groups seems very similar. Thus, like the feeding effects, both weanlings and adults can be demonstrated to be influenced by wheel access, though there is a much larger effect on body weight in adults. From the trend evident in the last experiment it is possible to speculate that if wheel access had been maintained longer, the differences in weight between the two groups of weanling rats might have become more pronounced and proven significant.

General Discussion

The focus of this study was to investigate the effect of ad lib wheel access on feeding behaviours and weight regulation of adult male and female rats, and of weanling male rats. Adult males and females increased running at about the same rate, but females ran much more than males by days 11-15. This gender difference in running is well known (Cortright et al., 1997; Eikelboom & Mills, 1988; Lambert & Kinsley, 1983; Richter, 1927; Slonaker, 1908; Tokuyama et al., 1982; Wang, 1923). In adult and weanling males, running was similar, increasing at the same rate and plateauing at the same level, despite the large weight difference in these animals. The similarity in running between adult and weanling males has not been explicitly demonstrated before.

Adult males and females when given wheel access, show a similar degree of feeding suppression that recovered at about the same time. The rats lost weight as consequence of the decreased food intake and increased activity. After the initial loss of weight, the male and female animals with wheel access maintained their weight at a similar percentage (92% vs. 88%, respectively) of their corresponding controls, although food intake rebounded to sedentary levels of consumption.

The effect of age on wheel access was explored by comparing adult and weanling males. While in adults wheel access suppressed feeding and reduced weight, weanling males showed greatly attenuated effects of wheel access. There was a small feeding suppression (only 16% at its maximum relative to 38% in adults), but this effect occurred in the face of rapidly increasing food intake in controls. In adults the effects of wheel access occurred while controls showed more or less stable feeding. Effects of wheel access on body weight in weanlings was less severe than the effects of wheel access on weight in adults. In the weanlings, the weight reduction (relative to controls) was small and temporary, but there were suggestions that at adulthood, weanlings given wheel access might come to show a weight suppression relative to their controls. Both findings of reduced food intake and weight become non-significant when compared to adult males.

In reviewing the literature on wheel running effects on feeding and weight, it appears that some of the conflicts in the literature are due to comparisons that confound sex and age. In this discussion, I will first examine the literature comparing the effects of exercise in adult male and female rats and how the this study relates to that literature. Then I will discuss the confound of age in previous work, and finally the implications of these findings for human weight regulation and eating disorders will be explored.

Voluntary wheel running studies using female rats have found inconsistent results (similar to forced exercise literature, see Appendix). The present study did not find a sexually dimorphic difference in feeding and weight gain for the WH rats compared to NW rats. In this study, both males and females with wheel access suppressed feeding initially and regulated their weight at a reduced level compared to sedentary controls. Jones et al. (1990) and Tokoyama et al. (1982) found that wheel running initially elicited a decrease in ad lib food intake and a decrease in body weight for both males and females. In contrast, Pitts (1984) and Cortright et al. (1997) reported that voluntary wheel running was not associated with a suppression in feeding in females and was associated with a decrease in body mass in male but not female (Sprague-Dawley) rats.

The rats studied by Tokuyama et al. (1982), Jones et al. (1990), and the present Experiments 1 and 2, began running as adults (50+ days old), whereas, in the Pitts (1984) and Cortright et al. (1997) studies, the rats began to exercise as weanlings (21 days old). Thus, it seems age may be an important factor in the inconsistencies found in the literature.

In Experiment 3, there was evidence of a very small feeding suppression and minor reduced weight with initial wheel access; however, compared to Experiment 1 (and 2) it was not significant. As mentioned before, this was probably due to the rapid growth period experienced by the weanlings. Cortright et al. (1997) and Pitts (1984) employed weanlings as well. They did not report a hypophagia or reduced weight gain with initial wheel access; however, Cortright et al., (1997) did their analysis on weekly means and Pitts (1984) on 10 day means. Thus all studies with weanlings find wheel access has no initial effects on feeding or weight.

Although in Experiment 3, the weanling WH rats only showed a short mild feeding suppression compared to NW controls (when only weanlings were considered), after the initial weight reduction they continued to gain weight at a similar rate as their NW controls, despite the dissimilar rate of energy expenditure. The adult male rats given wheel access almost immediately (significant on day 6) regulated their weight at a reduced level in comparison to the NW controls. The weanling WH rats of this study did not show this immediate weight suppression. Cortright et al. (1997) found that it took seven weeks of wheel access before the male weanlings showed a significant weight reduction relative to their controls and they found weight reduced gradually.

The comparison of adult to weanling males within the same paradigm on measures of food intake and weight gain with wheel access have not previously been performed. Thus, there may be a delayed weight reduction (as suggested by Cortright et al., 1997) and this reduction is not as rapid compared to weight effects for adults given wheel access in adulthood.

In the discussion of the age confound, it seems that the inconsistencies found between previous studies investigating sex differences in the effect of the wheel on weight may be demonstrating a difference in the age of animals used. The studies by Cortright et al. (1997) and Pitts (1984) showed that weanling males given wheel access displayed a weight reduction in adulthood, but weanling females did not. The present study, as other studies using older animals (e.g., Goodrick, 1980; Tokuyama et al., 1982), demonstrated that adult males and females show a weight reduction. Finding a sex difference with wheel running in one study and not in another may be a reflection of the age of the animals employed, not inconsistencies in the literature.

Wheel running at an early age when weight gain is rapid may impact development in a way that reduces its impact on weight gain. Energy expenditure initiated at different developmental stages may also affect weight or weight regulation in a similar manner. The mechanism responsible for this mild temporary initial weight reduction in weanlings is not obvious, but there are hormones that change their response in adulthood (e.g., growth hormones). The activational effects of hormones during this growth period may block the mechanisms responsible for weight reduction with early chronic exercise. Further studies are clearly needed to elucidate the effects of chronic exercise on hormones and control of growth during endurance exercise training in young rats. The difference between weanlings and adults in the effects of wheel access has its peak incidence just after adolescence. Children seem to be protected from this disorder. If wheel access models some aspects of the human disorder, it suggests age differences in incidence may have a biological basis. However, making conclusions about human eating disorders from this study needs to be made with considerable caution. The comparison made in the present study between male and female rats and young and old male rats may be of relevance to demographical variables involved in biological control of anorexia nervosa.

The results of Experiment 1 and 2 indicate that there is an inverse relationship between initial physical activity and feeding, eating is suppressed with increased exercise. Similar behaviourial interactions between feeding and exercise have been found in recent clinical studies with eating-disordered patients (see, Davis, 1997), which suggests that physical activity plays a more central role in the development and maintenance of the eating disorder than had previously been thought. There is an overwhelming preponderance of women with anorexia nervosa (e.g., see Goodwin, Fairburn, & Cowen, 1987; Steiger, 1989). Given that no difference was found in the male and female comparison of this study, our data does not support a role of biological factors in anorexia nervosa. While the gender difference in incidents of anorexia nervosa may have a social basis, the age differences seen in this study may have some importance on the possible explanation for onset of anorexia nervosa.. Adult animals (were just past puberty) showed a large suppression on feeding with wheel access. These differences parallel the age distribution in the first diagnosis of anorexia nervosa. Little evidence exists for anorexia nervosa in the period prior to puberty. After puberty, the incidence of anorexia nervosa increases with a few cases of onset observed later in adulthood. The later finding would suggest old rats should not show a feeding suppression with wheel access.

The results from this study suggest that further exploration of the differences between weanlings and adults in the effect of wheel access may be helpful in determining why the disorder is first evident in adolescence. Further research is needed to fully understand the interconnection between exercise and feeding in rats. This may shed light on the prevalence of anorexia nervosa and determine its neurobiological basis.

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Table 1

Summary of significance levels for the Sex X Group X Days ANOVA of weight changes for the comparison of Experiment 1 and Experiment 2

Source	D1-5	D6-10	D11-15	Explanation
Sex	.001	.001	.001	Males weigh more than females
Group	–	.02	.004	NW group weighs more than WH group
Days	.004	.001	.001	Weight increased over days
Sex X Group	–	–	–	
Sex X Days	.001	.001	.004	Males increased weight more rapidly than females
Group X Days	.001	.04	–	Wheel effect becomes evident
Sex X Group X Days	–	–	–	

Note. Dashes indicate the result was not significant.

Table 2

Summary of significance levels for the Age X Group X Days ANOVA of weight changes for the comparison of Experiment 1 and Experiment 3

Source	D1-5	D6-10	D11-15	D28-32	Explanation
Age	.001	.001	.001	.001	Adults weigh more than weanlings.
Group	—	.02	.04	.05	NW group weighs more than WH group.
Days	.001	.001	.001	.001	Weight increased over days.
Age X Group	–	–	–	–	
Age X Days	.001	.001	.001	.001	Weanlings increased weight more rapidly than adults.
Group X Days	.001	–	–	–	Group difference is evident over the first few days.
Age X Group X Days	.001	–	–	–	The effect of wheel access is more pronounced in adults.

Note. Dashes indicate the result was not significant.

Figure Captions

Figure 1. Mean (±SEM) number of adult male rat wheel turns per 12 hours of the dark cycle. Days 16-21 was based on only one replication (n = 3).

Figure 2. Mean (±SEM) number of 45 mg food pellets consumed per 12 hours of the dark cycle by adult male rats in active and sedentary groups. Days 16-21 was based on only one replication (wheel access group, n = 3; no wheel access group, n = 4).

Figure 3. Mean (±SEM) of body weight in grams for adult male rats in active and sedentary groups.

Figure 4. Mean (±SEM) number of adult female rat wheel turns per 12 hours of the dark cycle.

Figure 5. Mean (±SEM) number of adult female and male rat wheel turns per 12 hours of the dark cycle.

Figure 6. Mean (±SEM) number of 45 mg food pellets consumed per 12 hours of the dark cycle by adult female rats in active and sedentary groups.

Figure 7. Mean (±SEM) number of 45 mg food pellets consumed per 12 hours of the dark cycle by adult female and male rats in active and sedentary groups.

Figure 8. Mean (±SEM) of body weight in grams for adult female rats in active and sedentary groups.

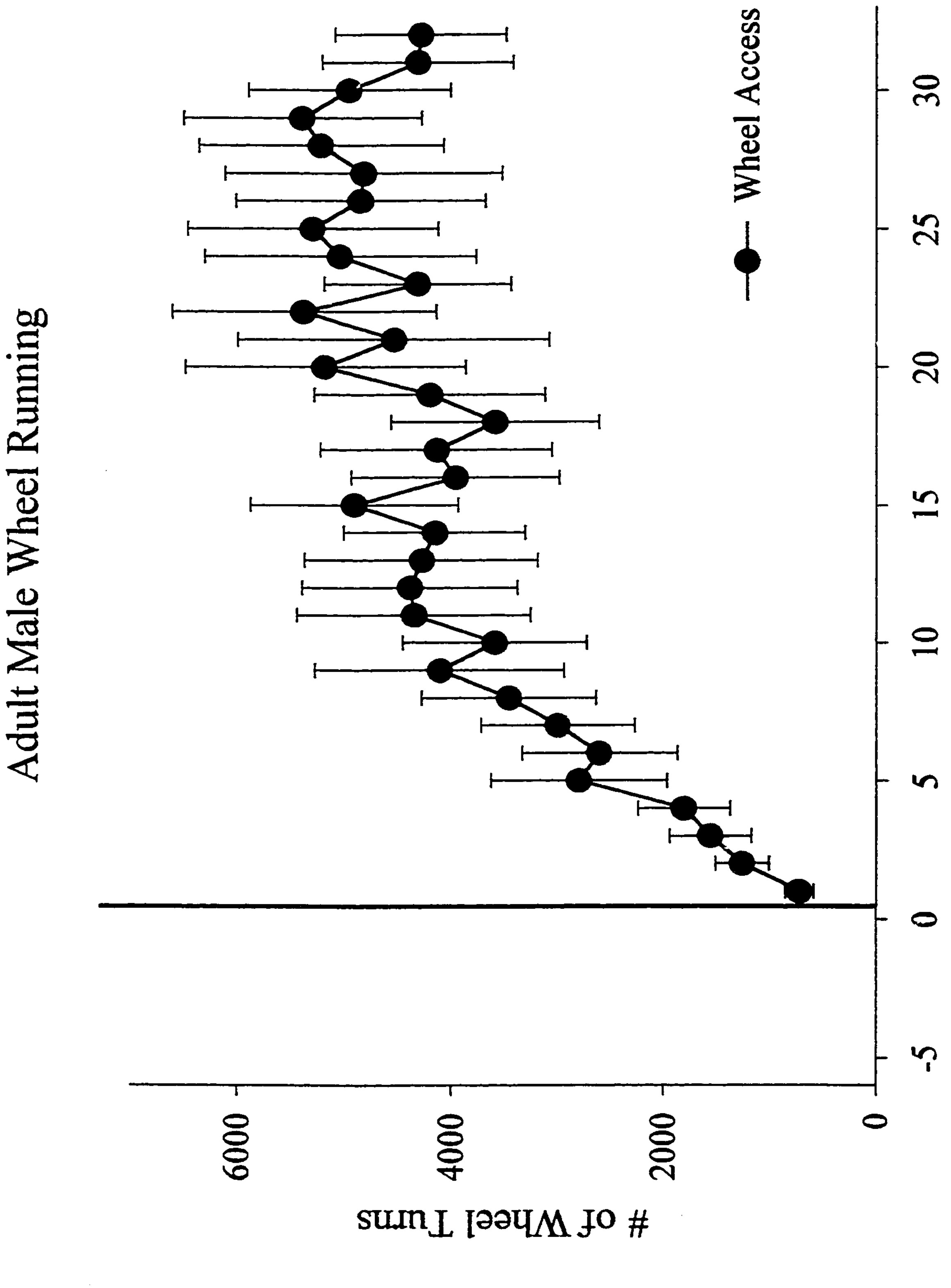
Figure 9. Mean (±SEM) of body weight in grams for adult female and male

and females may react differently to the extra effects of the forced exercise.

First, the stress response has been shown to be sexually dimorphic. Forced running , with restricted food intake, results in more stomach ulceration in female than male rats (Robert, Northam, Nezamis & Phillips, 1970), while with other types of stress protocols the sex differences may be reversed, with males affected more than females (Sawrey & Long, 1962). Thus, it is important to be cautious when interpreting results from forced exercise and then comparing them to voluntary wheel running. The stress experienced by a male or female rat could be different depending on the protocol.

Second, the intensity of wheel running and forced exercise differ and this may explain why in forced exercise there may be a sex difference that was not seen in the present study with wheel running. Rats in running wheels typically exercise intermittently throughout the dark cycle. This behaviour may represent a lower intensity stimulus than would occur with forced treadmill exercise. It may be that because the exercise protocol is usually the same for males and females, the forced treadmill running does not challenge females. With voluntary wheel running, females run more than males over the 12 hours of the dark phase. Eikelboom and Mills (1988) found that females ran for longer durations per running episode and at a greater speed than males. As discussed earlier, Mayer et al.(1954) found feeding effects differed depending on the duration of forced running. Perhaps the methodology for forced exercise studies needs to take into account the sex differences and increase the intensity of running, by increasing the duration and speed at which the females are forced to exercise.

Figure 1


Adult Male Wheel Running
# of Wheel Turns
0
2000
4000
6000
Days
-5
0
5
10
15
20
25
30
Wheel Access

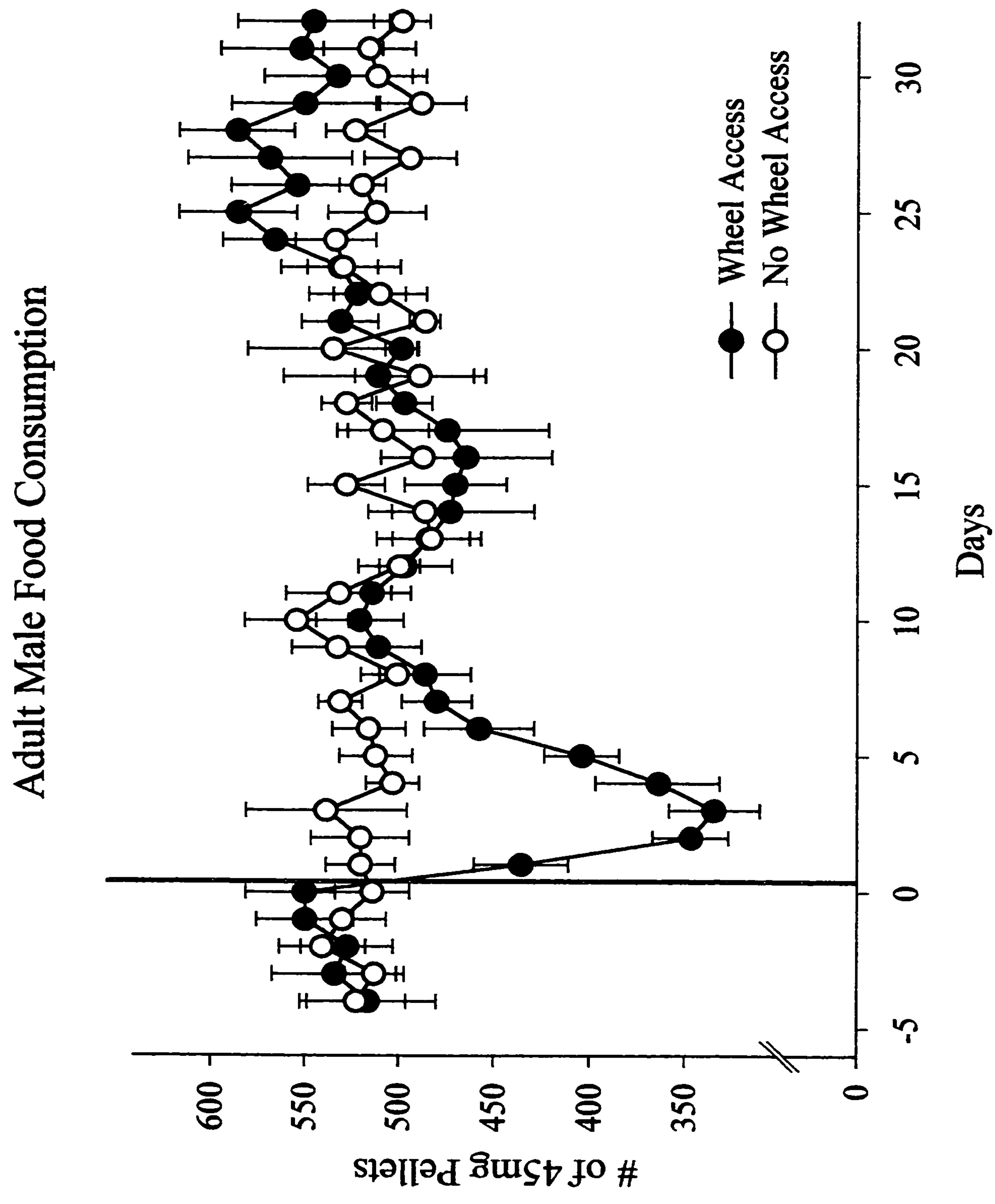

Adult Male Food Consumption
# of 45mg Pellets
600
550
500
450
400
350
0
-5
0
5
10
15
20
25
30
Days
Wheel Access
No Wheel Access

Figure 2

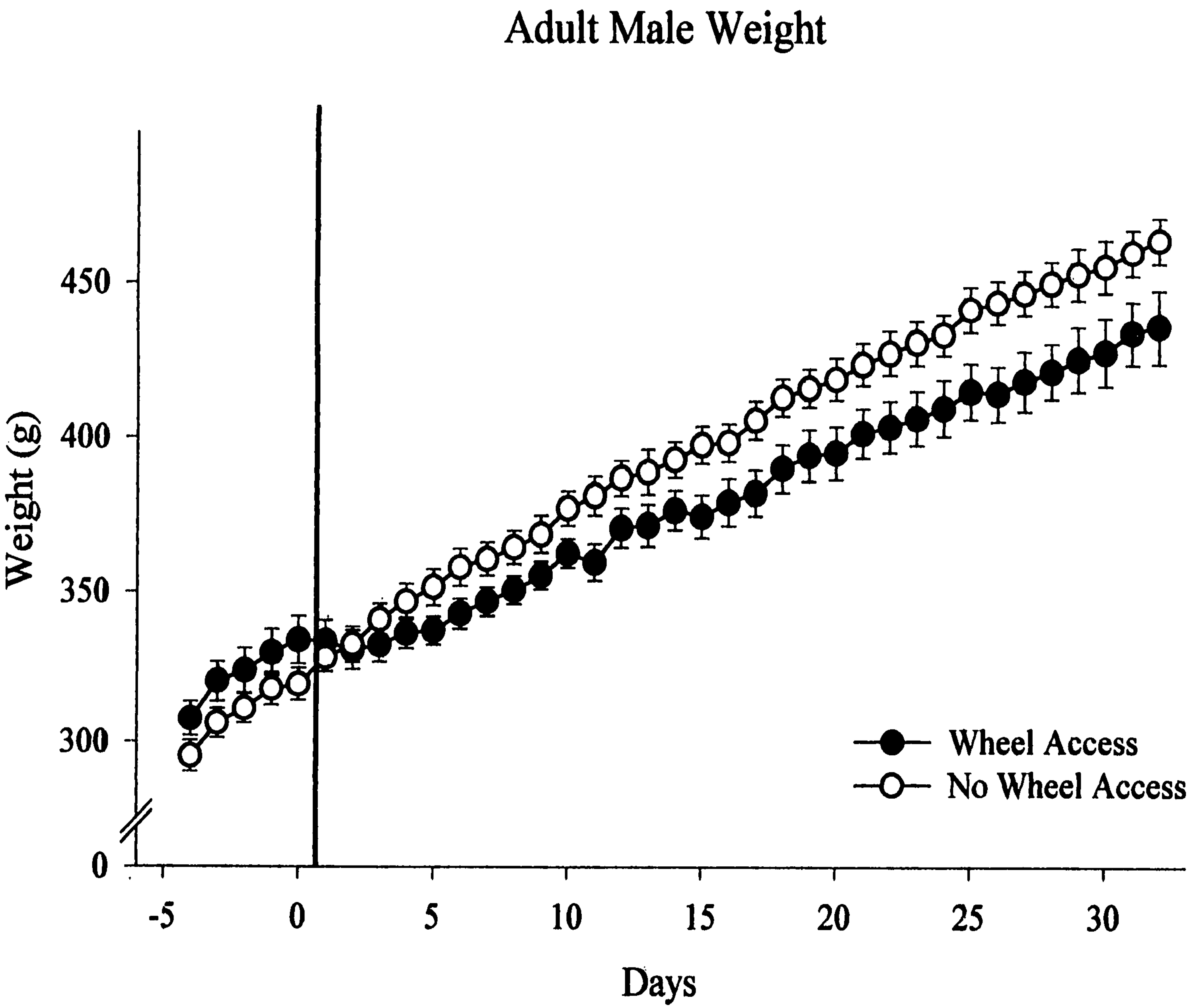
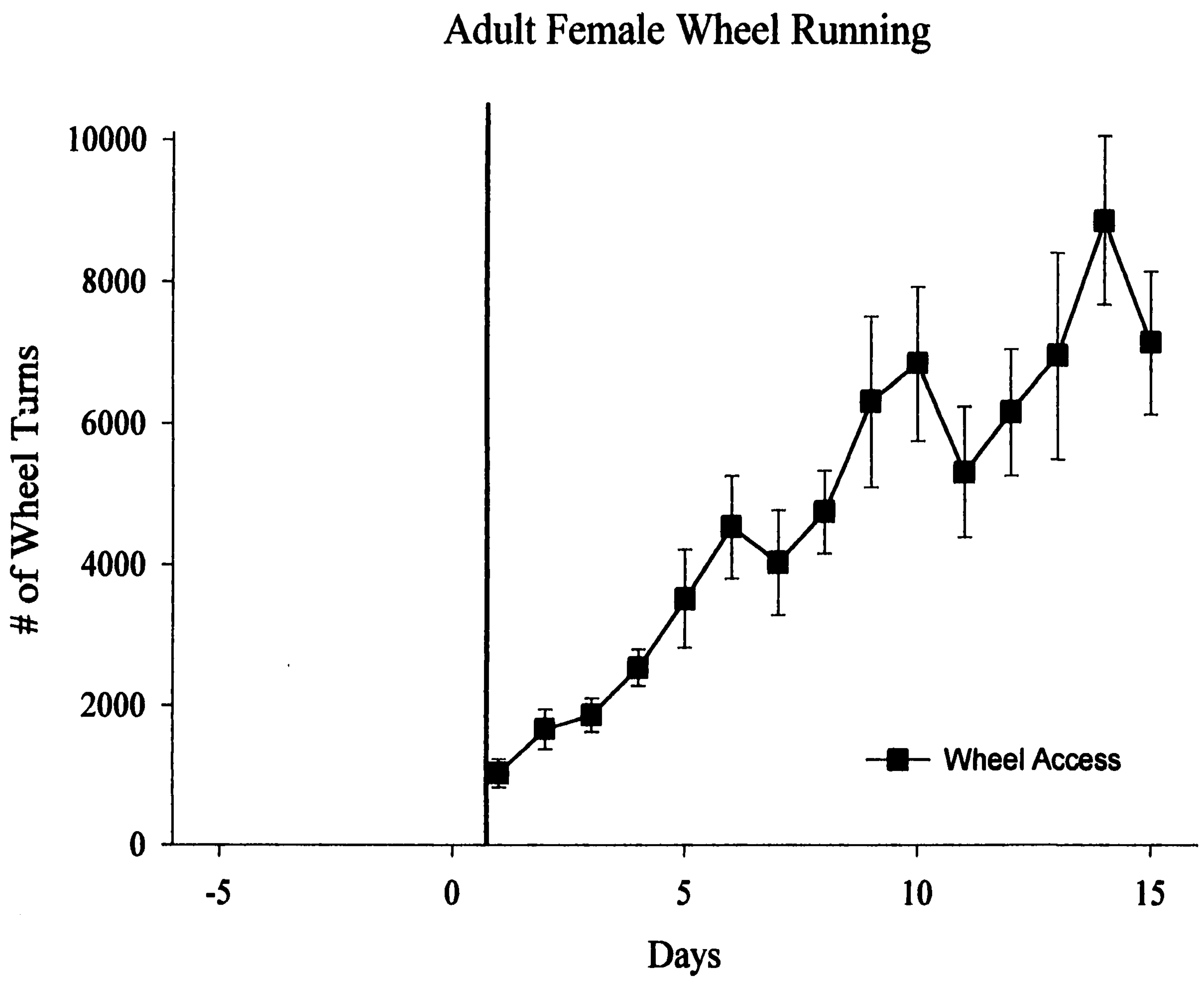

Adult Male Weight
Weight (g)
0
300
350
400
450
-5
0
5
10
15
20
25
30
Days
Wheel Access
No Wheel Access

Figure 3



Adult Female Wheel Running

Figure 4

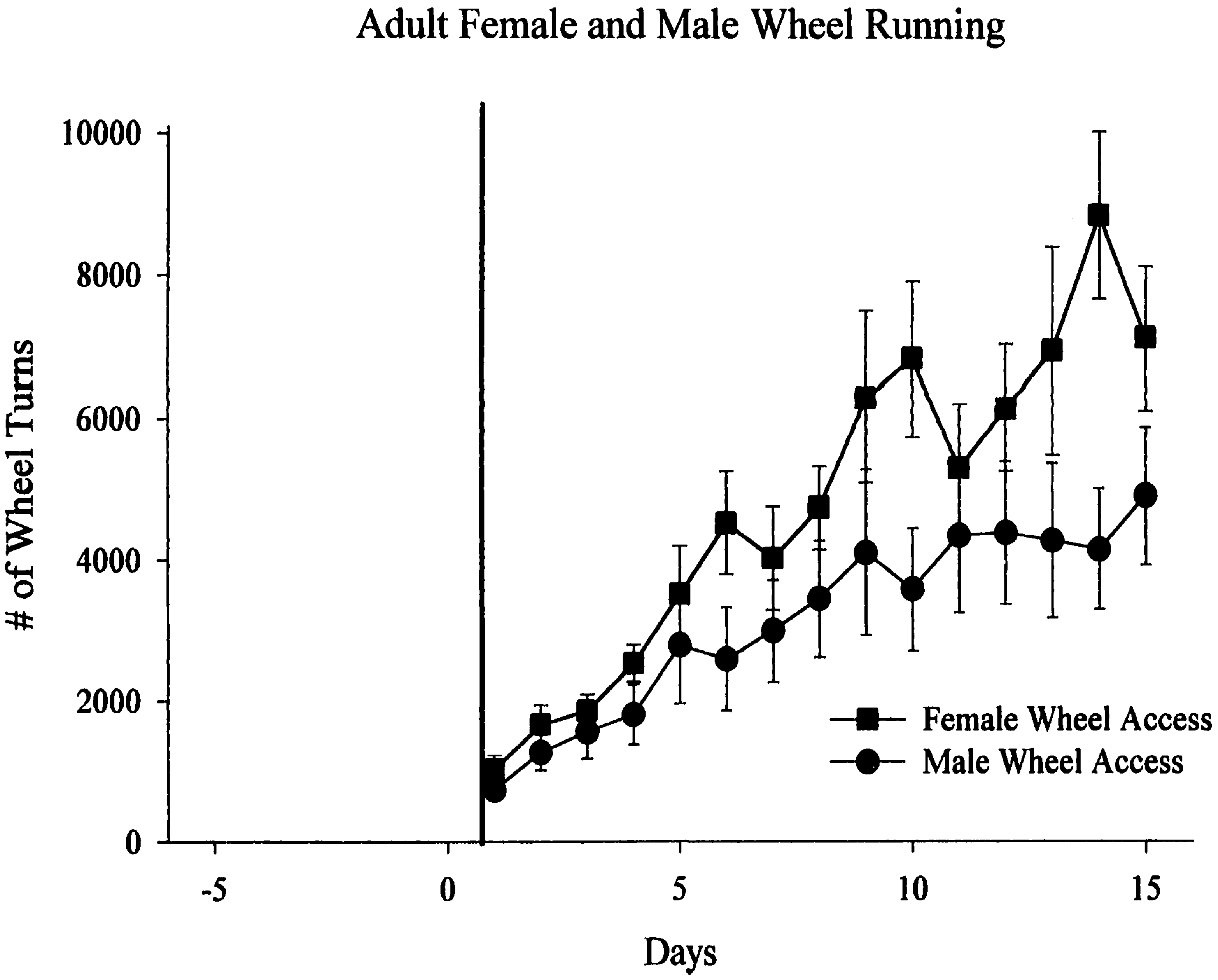
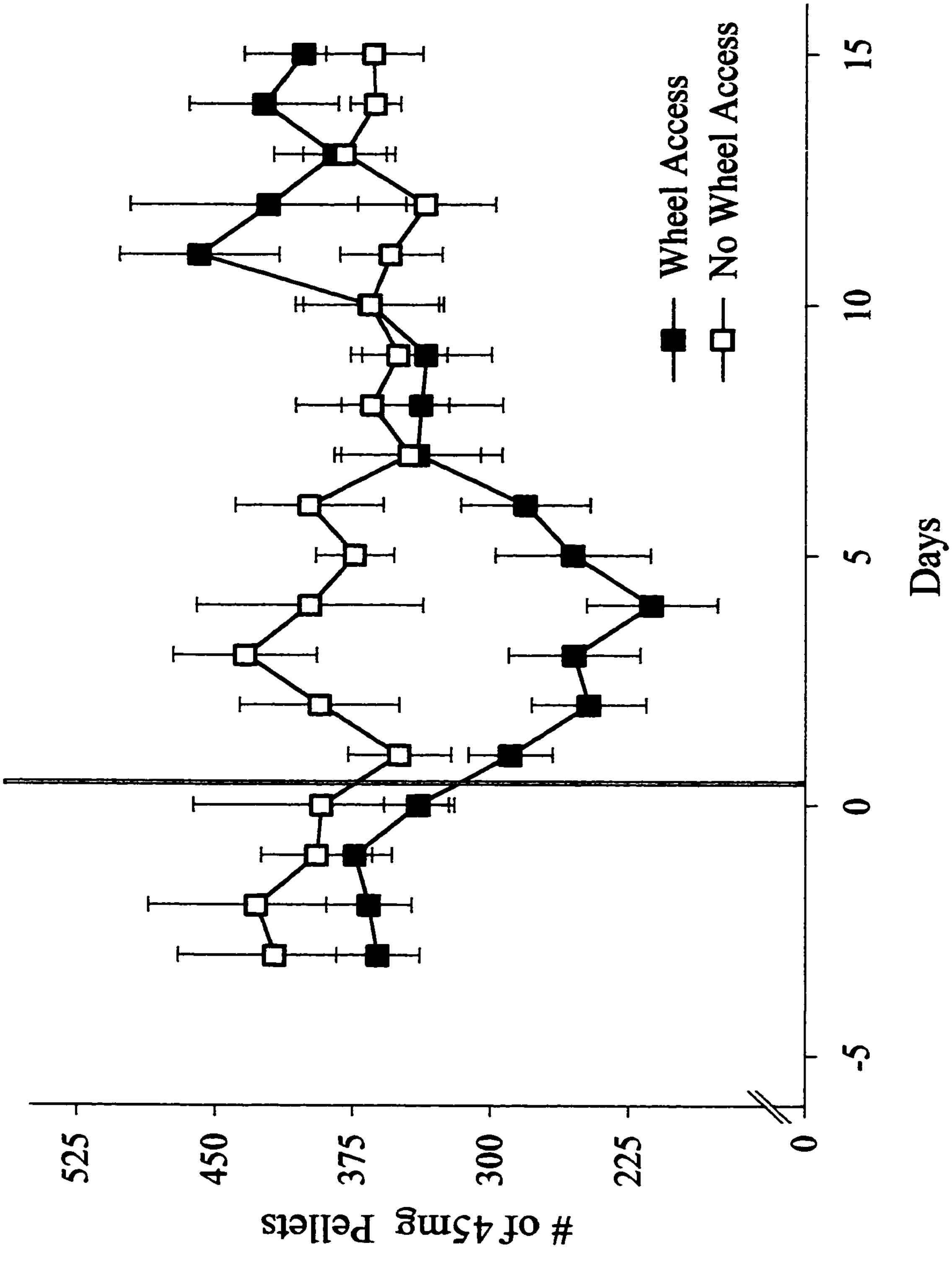

Adult Female and Male Wheel Running
# of Wheel Turns
10000
8000
6000
4000
2000
0
-5
0
5
10
15
Days
Female Wheel Access
Male Wheel Access

Figure 5

Figure 6

Adult Female Food Consumption



Adult Female and Male Food Consumption

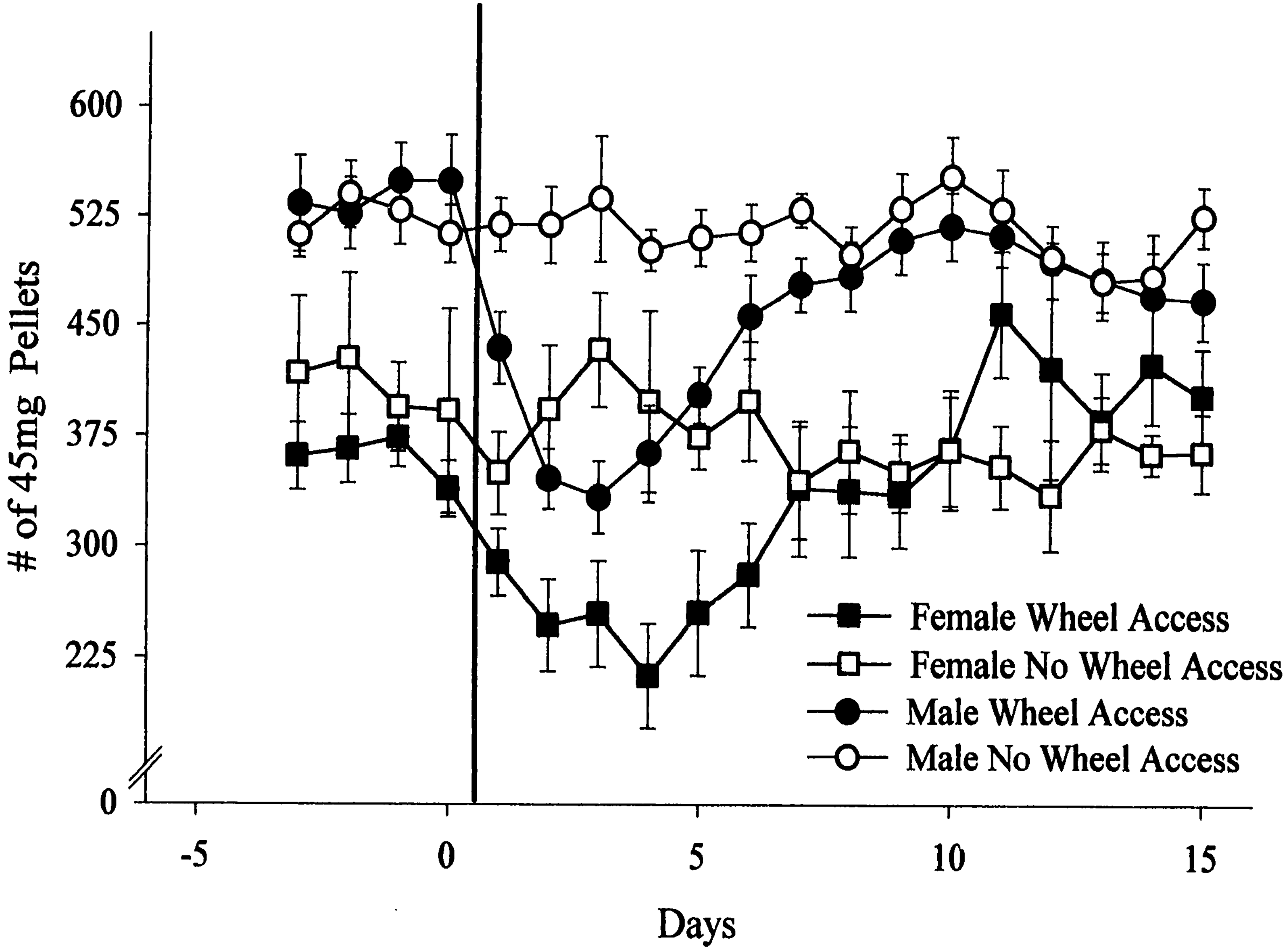


Figure 7

Figure 8

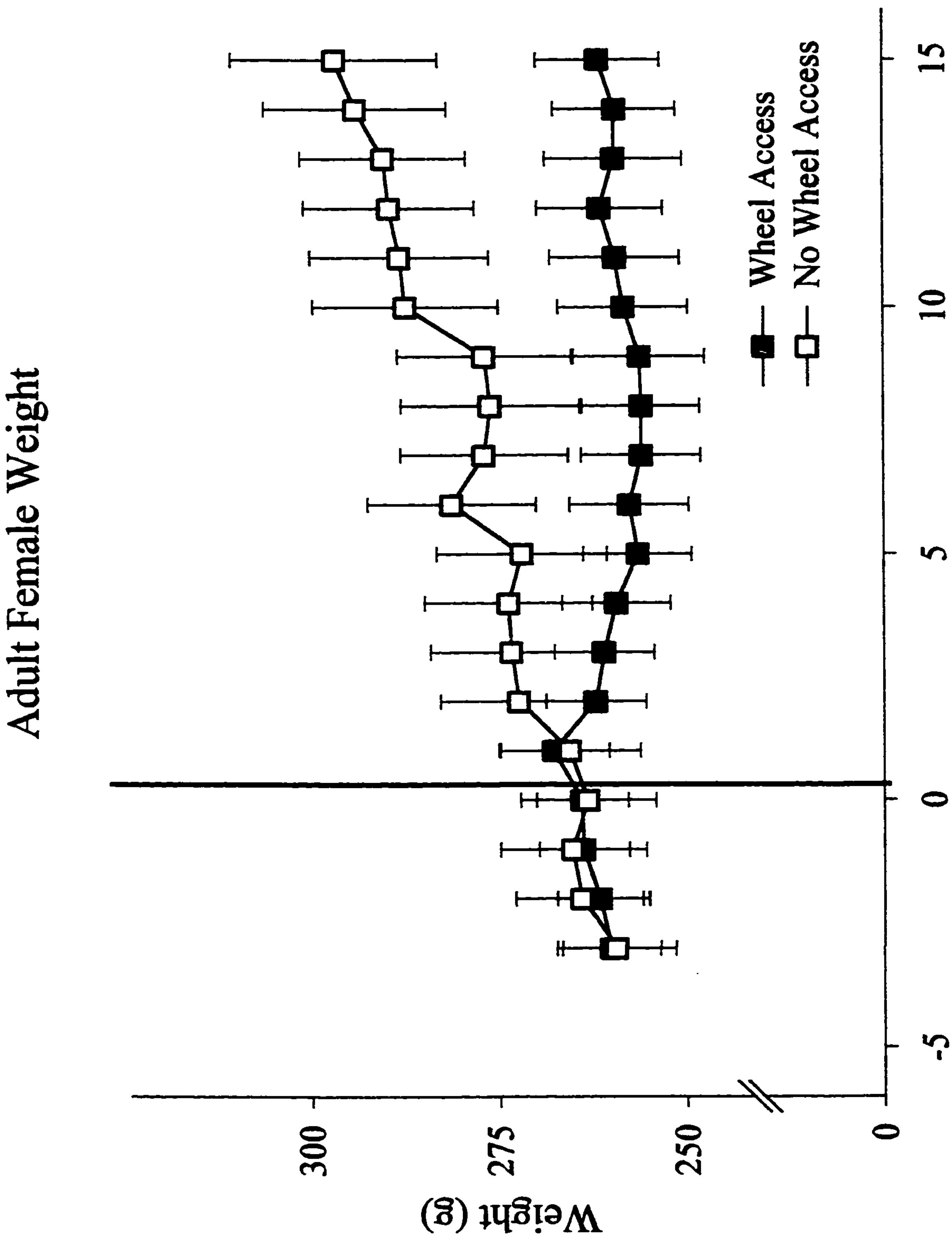

Adult Female Weight
Weight (g)
300
275
250
0
-5
0
5
10
15
Days
Wheel Access
No Wheel Access

Figure 9

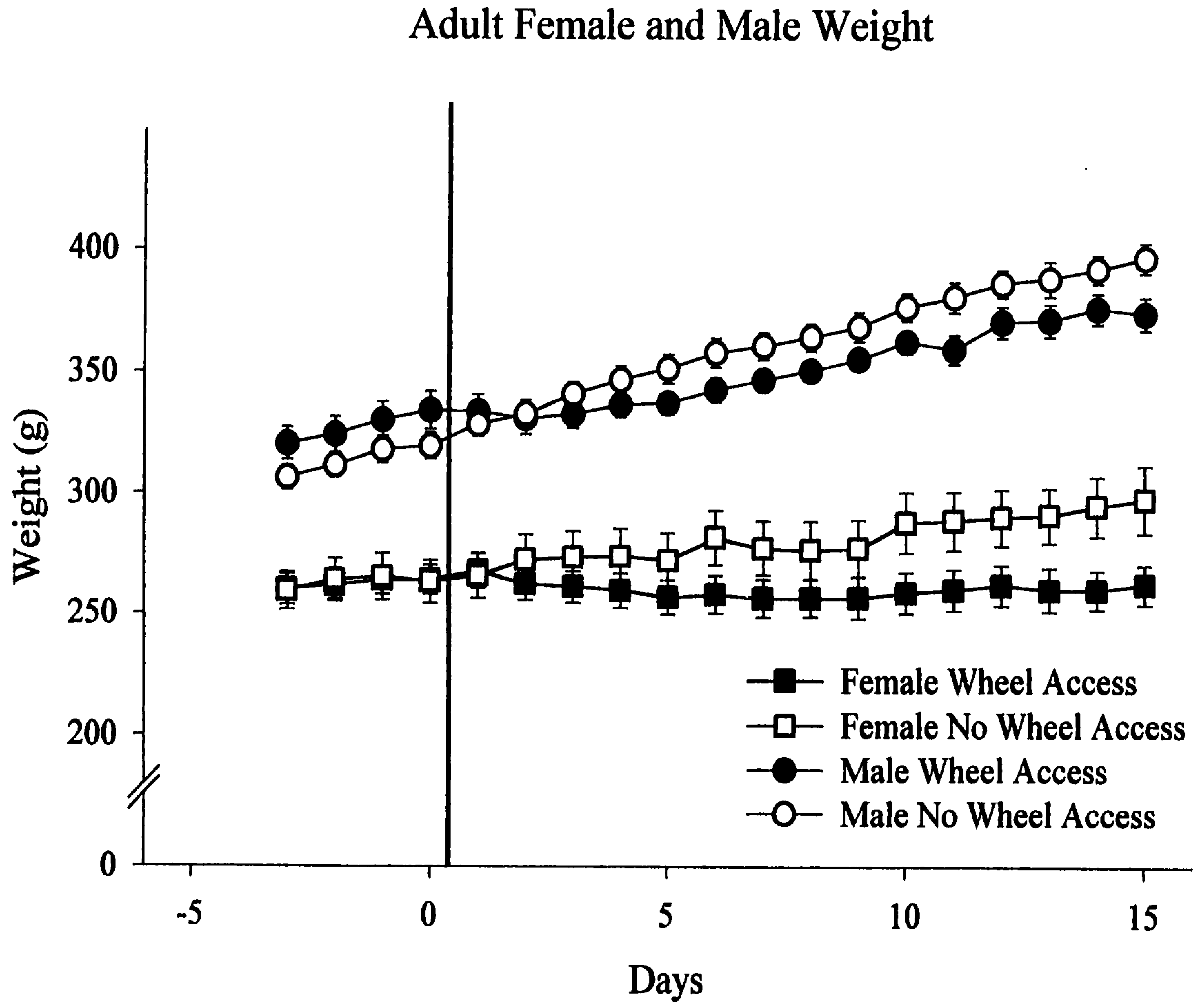

Adult Female and Male Weight
Weight (g)
400
350
300
250
200
0
-5
0
5
10
15
Days
Female Wheel Access
Female No Wheel Access
Male Wheel Access
Male No Wheel Access

Figure 10

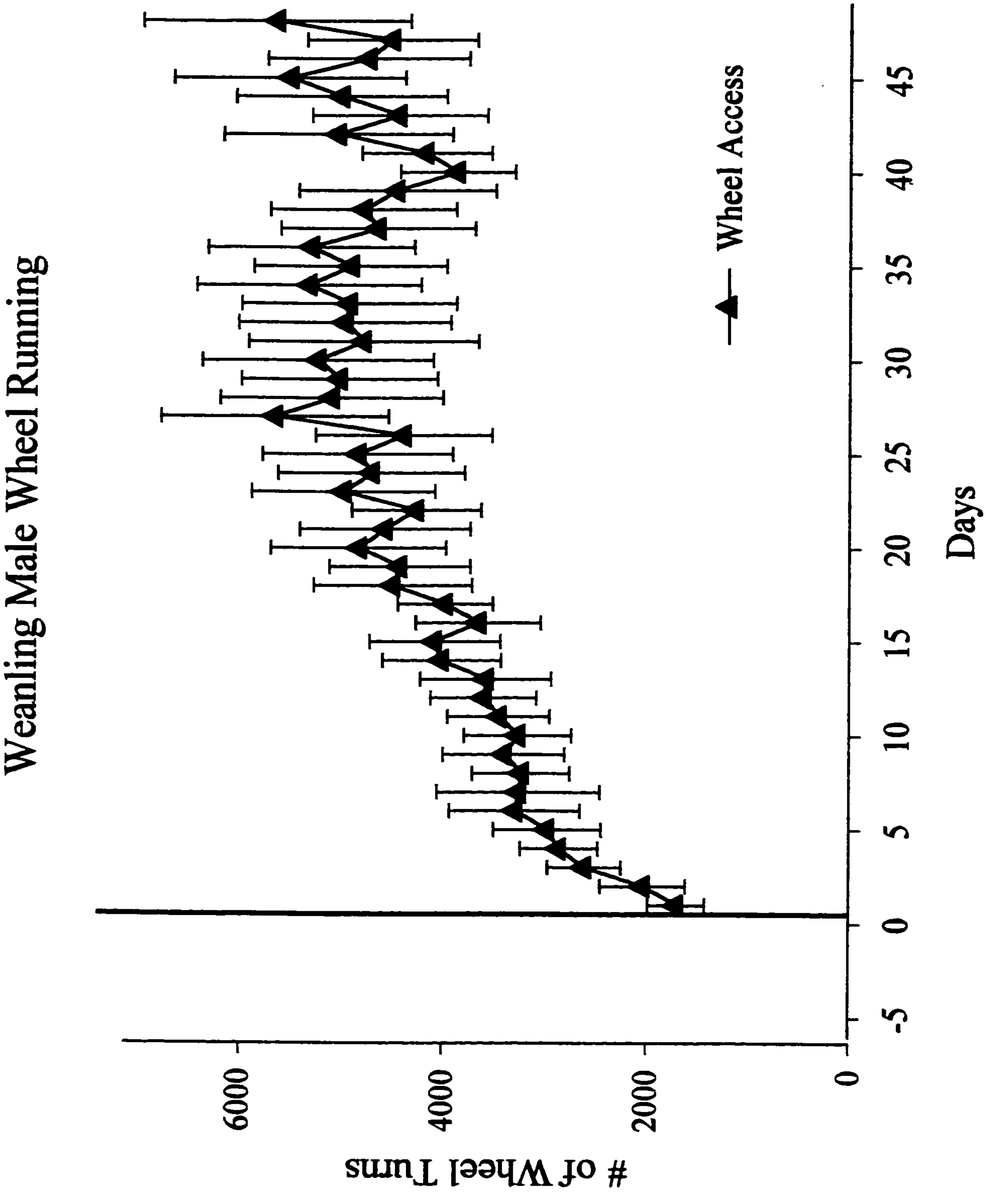

Weanling Male Wheel Running
# of Wheel Turns
6000
4000
2000
0
-5
0
5
10
15
20
25
30
35
40
45
Days
Wheel Access

Figure 11

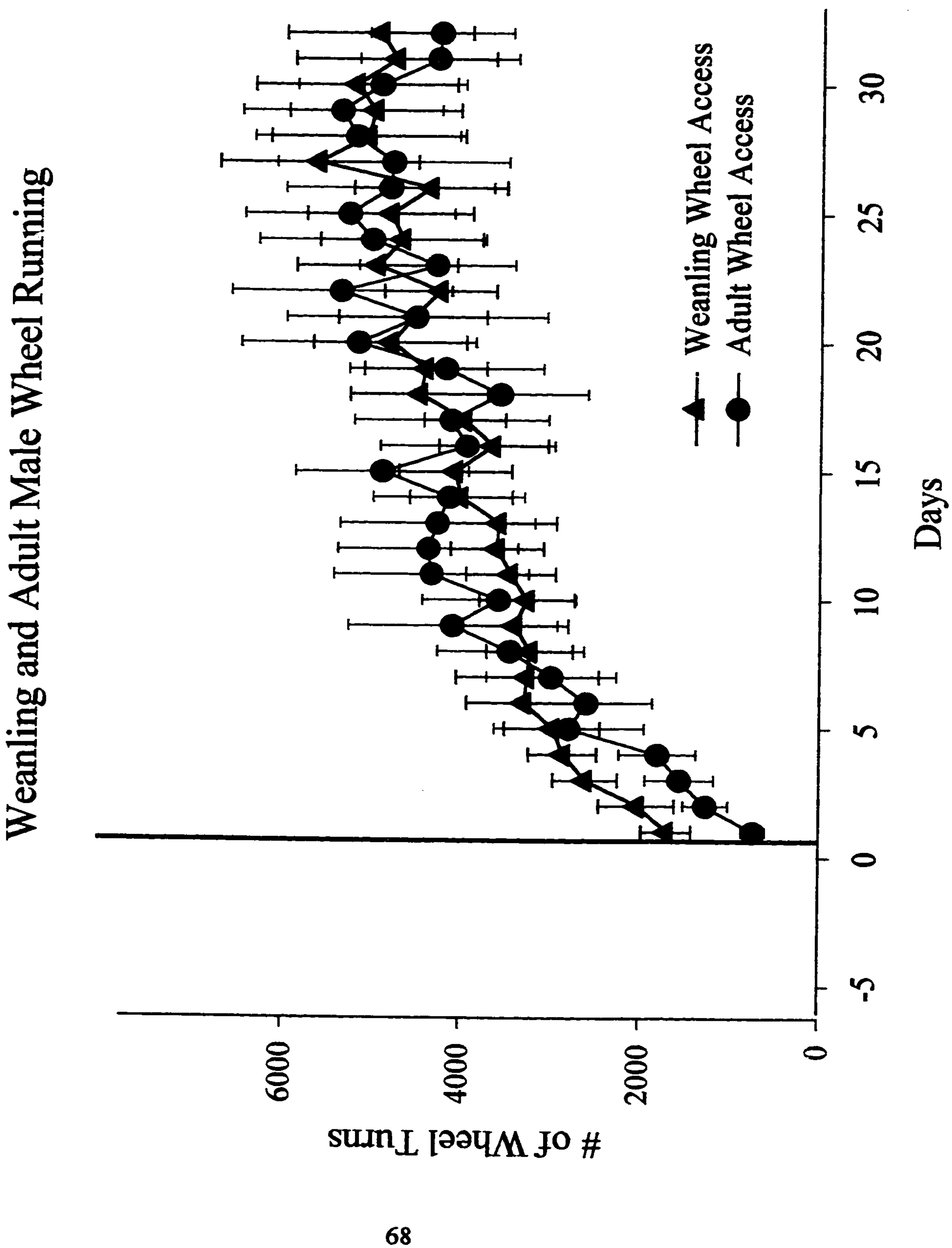

Weanling and Adult Male Wheel Running
# of Wheel Turns
0
2000
4000
6000
-5
0
5
10
15
20
25
30
Days
Weanling Wheel Access
Adult Wheel Access

Figure 12

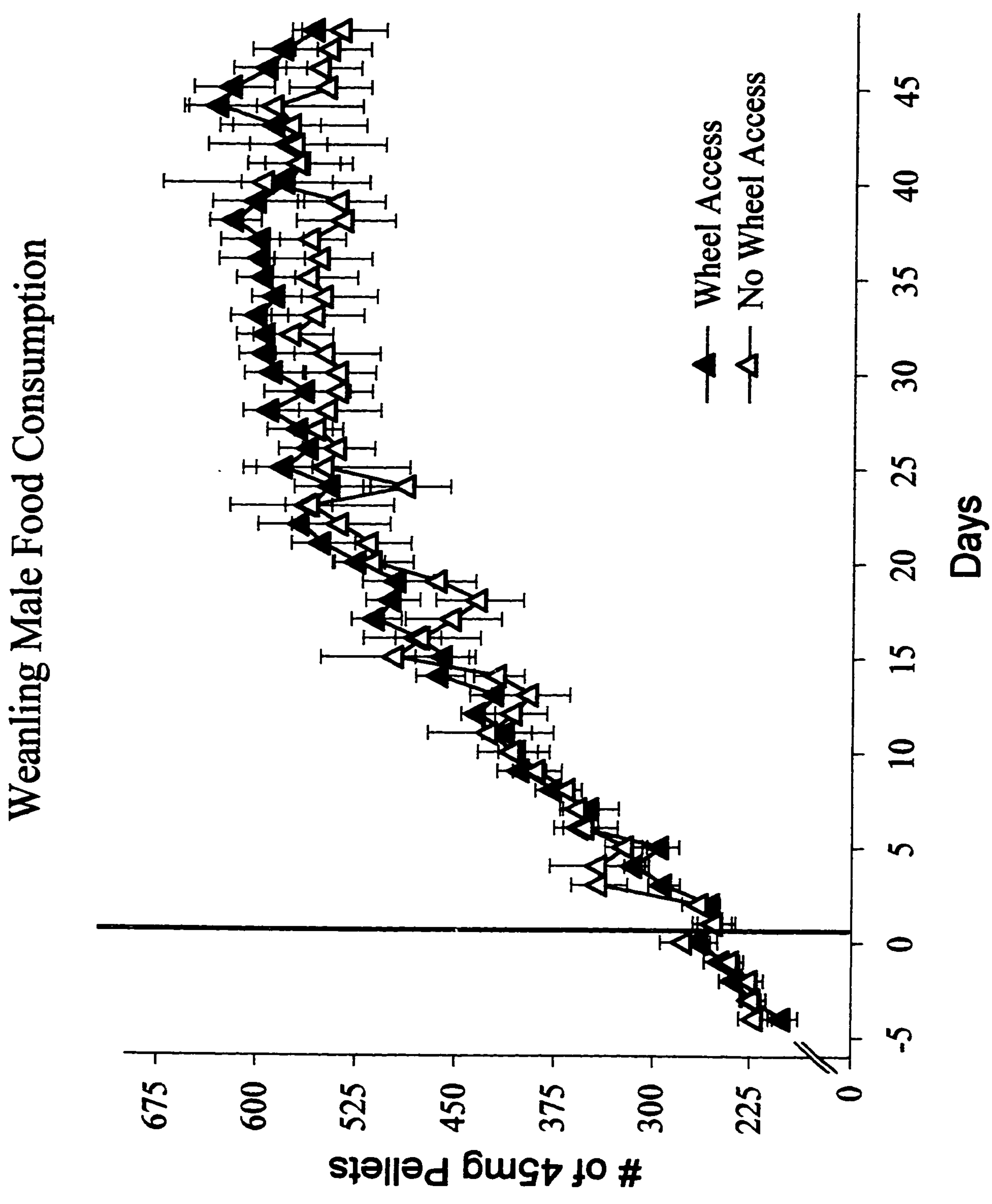

Weanling Male Food Consumption
# of 45mg Pellets
0
225
300
375
450
525
600
675
Days
-5
0
5
10
15
20
25
30
35
40
45
Wheel Access
No Wheel Access

Figure 13

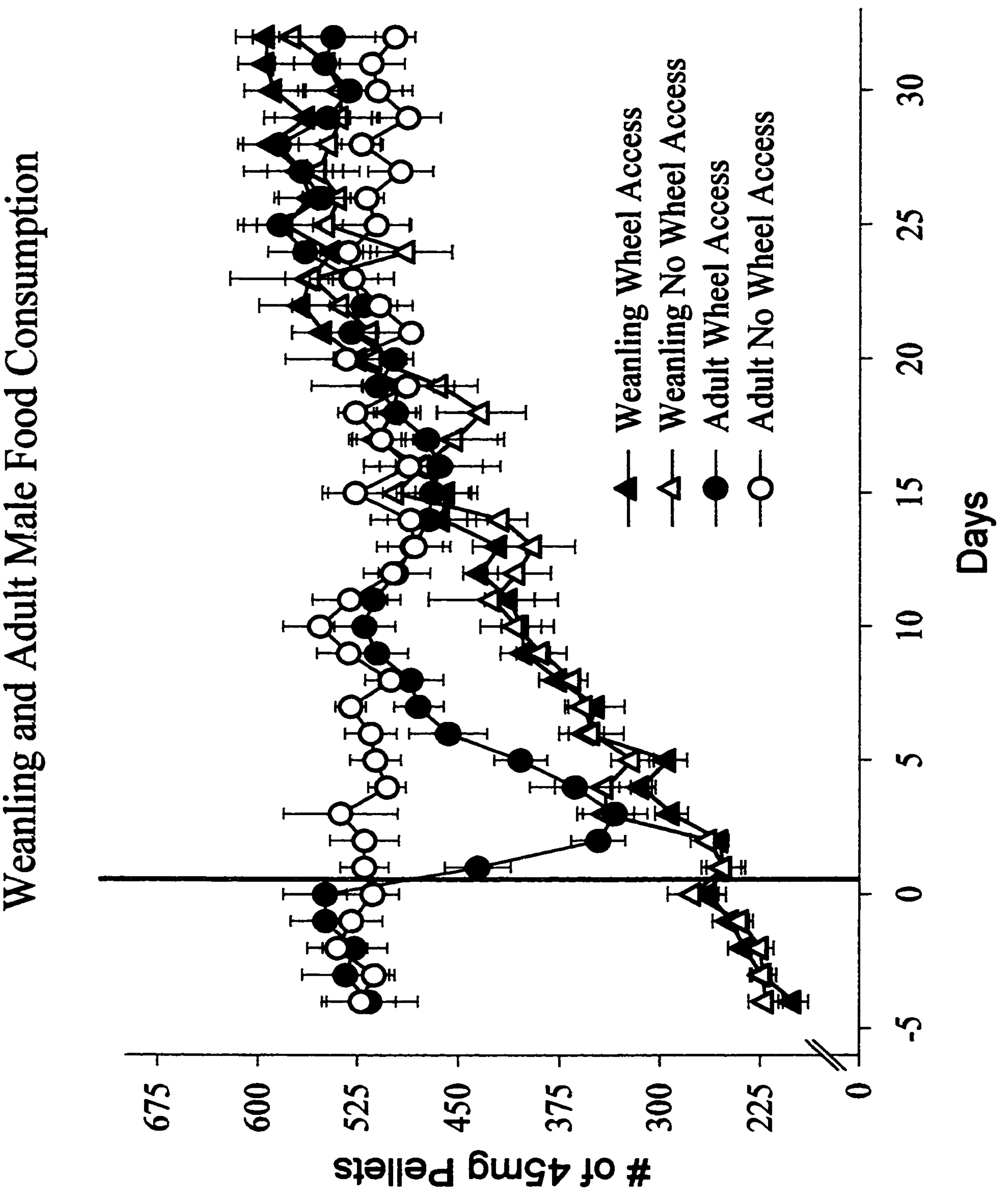

Weanling and Adult Male Food Consumption
# of 45mg Pellets
675
600
525
450
375
300
225
0
-5
0
5
10
15
20
25
30
Days
Weanling Wheel Access
Weanling No Wheel Access
Adult Wheel Access
Adult No Wheel Access

Figure 14

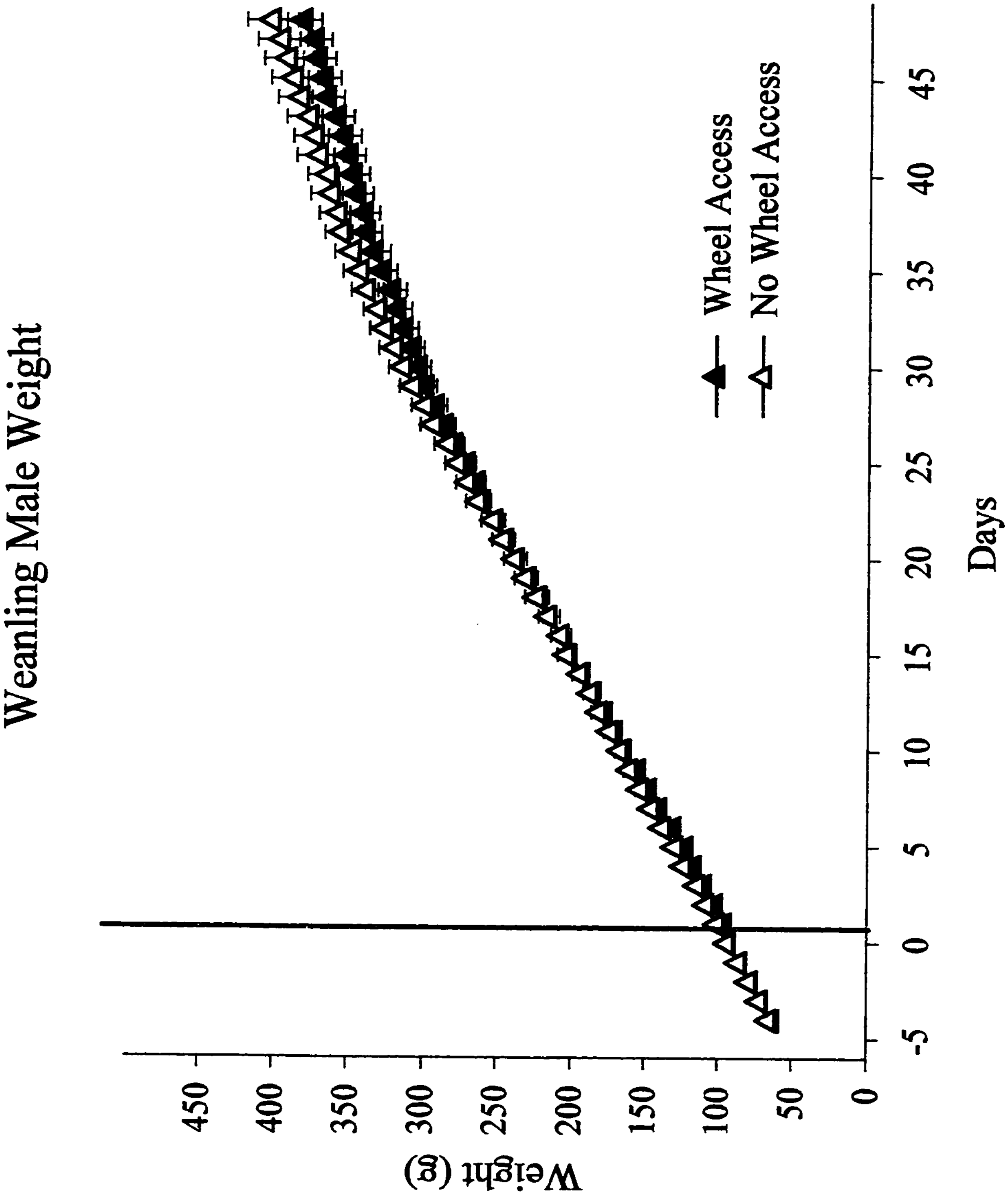
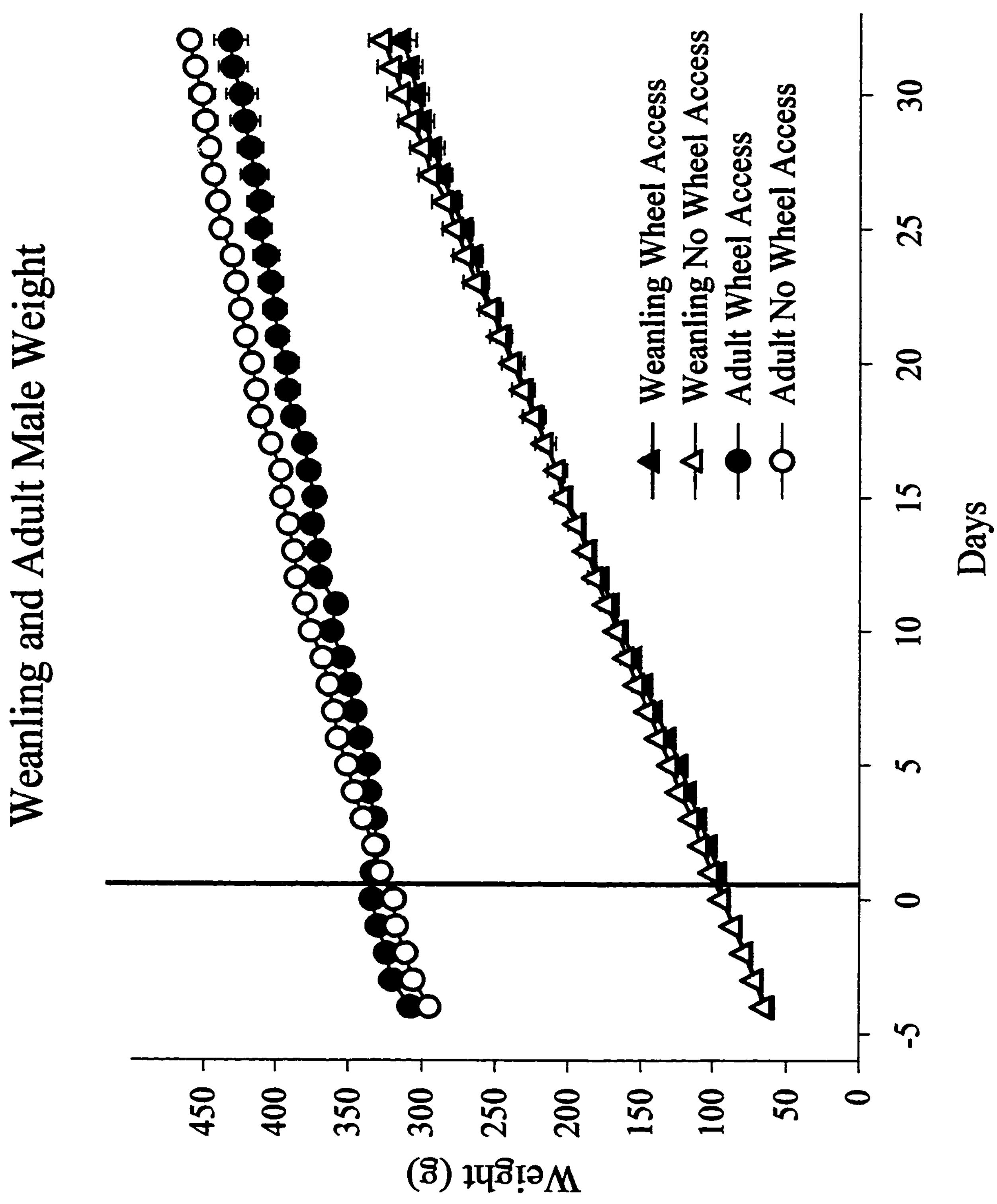

Weanling Male Weight
Weight (g)
0
50
100
150
200
250
300
350
400
450
Days
-5
0
5
10
15
20
25
30
35
40
45
Wheel Access
No Wheel Access

Figure 15


Weanling and Adult Male Weight
Weight (g)
0
50
100
150
200
250
300
350
400
450
Days
-5
0
5
10
15
20
25
30
Weanling Wheel Access
Weanling No Wheel Access
Adult Wheel Access
Adult No Wheel Access