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Physical Activity and Food Consumption in High- and Low-Active Inbred Mouse Strains

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Abstract

Purpose—To determine the effect of innate activity level and running wheel access on food consumption in high-active (SWR/J) low-active (DBA/2J) mice.

Methods—Two strains of inbred mice were used in this study due to their high activity level (SWR/J) and low activity level (DBA/2J). The mice were housed in individual cages, and half of the mice in each strain had free access to running wheels in their cages, while the other mice received no running wheel. All mice consumed standard chow and water *ad libitum* for 13 weeks during the study period. Running-wheel activity (daily), food consumption (bi-weekly), and body mass (weekly) were recorded.

Results—SWR/J runners consumed more food (6.0 ± 0.4 g/day) than SWR/J non-runners (4.7 ± 0.2 g/day; $p=0.03$), DBA/2J runners (4.6 ± 0.2 g/day; $p=0.02$), and DBA/2J non-runners (4.2 ± 0.2 g/day; $p=0.006$). SWR/J non-runners consumed more food than DBA/2J non-runners ($p=0.03$). Average daily distance and duration were significantly greater for the SWR/J runners (6.4 ± 0.7 km/day and 333.6 ± 40.5 min/day, respectively) compared to the DBA/2J runners (1.6 ± 0.4 km/day and 91.3 ± 23.0 min/day, respectively). There was a significant correlation between food consumption and distance ($r=0.74$, $p<0.001$), duration ($r=0.68$, $p<0.001$), and speed ($r=0.58$, $p<0.001$), respectively, in all mice. However, when considering the individuals strains, the relationship between running-wheel activity and food consumption was only statistically significant for the SWR/J mice.

Conclusion—Higher running-wheel activity in mice was associated with increased food consumption in the SWR/J mice but not the DBA/2J mice. In DBA/2J mice the addition of a running wheel did not result in increased food consumption, suggesting energy expenditure of non-wheel cage activity in the control DBA/2J mice was similar to the energy expenditure of the wheel activity since body mass was similar between the two groups.

Keywords

voluntary exercise; running wheel; SWR mice; DBA mice

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Introduction

The balance between food consumption and energy expenditure is essential to maintaining body mass (7). Past studies in male and female rodents have not consistently shown that increased physical activity has a positive effect on body mass, particularly when the training periods are of short duration (i.e. – less than 12 weeks) (8,10,20). However, in many cases a decrease, or attenuation of the increase, in body mass or body fat as a result of increased physical activity has been shown in both male and female rodents (3,4,23,25). Thus, the effect of activity on body mass or body fat loss appears to multi-factorial and does not appear to be limited to a single species or gender. Factors affecting the degree of weight loss include, but are not limited to, the duration of the study period, gender, age, rodent species, genetic influences on activity level, and/or energy intake (1,5,6,9,17,24).

In several studies, regardless of the effect on body mass, increased physical activity through use of running wheels or treadmills resulted in increased food consumption in rodents when food was provided *ad libitum* (4,6,7,12,24,25). However, many of these studies have used mouse strains that were highly active (ARC Swiss Albino), or bred to be highly active (24). Other studies using mouse strains that tend to be low-active, such as C57Bl/6 mice, have found no difference in food consumption, or time spent feeding, in mice exposed to running wheels (8,10). Thus, the innate running-wheel activity level of the rodents may influence food consumption. Additionally, mice that were forced to work for food tend to increase their activity (18,27). When the forced work was of low intensity or volume, the mice consumed a similar amount of food regardless of the activity required to obtain the food (18). However, if the activity required to obtain food was too high, it appears mice lost weight because the food consumption could not accommodate the high level of activity (18,27).

The interaction of running-wheel activity and food consumption is an understudied area. Therefore, the purpose of this study was to determine the effect of innate activity level and running-wheel access on food consumption in two inbred mouse strains, a high-active strain (SWR/J) and a low-active strain (DBA/2J).

Methods

All procedures were approved by the University Institutional Animal Care and Use Committee, and all procedures adhered to ACSM animal care standards. Ten female SWR/J mice and ten female DBA/2J mice were used in this study (Jackson Laboratories, Bar Harbor, ME). Female mice were used due to their ease in handling, compliance with physical activity tasks, and higher daily activity levels compared to male mice in these two strains (15,26). SWR/J mice were selected as the high-active strain, while DBA/2J mice were selected as the low-active strain (15,26).

All mice were housed in the University Vivarium with 12-h light/dark cycles with room temperatures and relative humidity standardized to 18-22° C and 20-40%, respectively. All mice were provided with water and standard chow (Harlan Teklad 8604 Rodent Diet, 24.5% protein, 4.4% fat, 3.7% fiber, and 48.6% nitrogen-free extract; Madison, WI) *ad libitum*.

At 9 weeks of age, all mice were housed in individual cages. Following one week of acclimation, half of each of the SWR/J mice (n=5) and the DBA/2J mice (n=5) received running wheels in their cages in order to measure daily running-wheel activity. The remaining SWR/J mice (n=5) and DBA/2J mice (n=5) were under identical conditions, but did not have running wheels in their cages. Each solid surface running wheel (145mm; Ware Manufacturing, Phoenix, AZ) was interfaced with a magnetic sensor and bicycle computer (BC600 Sigma Sport, Olney, IL) that counted the total number of wheel revolutions and total duration of exercise for each mouse (15,26). Wheel revolutions and time spent exercising were used to

measure distance (km) and duration (min), respectively, which were recorded daily for each mouse for 13 weeks beginning at 14 weeks of age. Technical difficulties associated with the running wheels necessitated data collection begin at 14 weeks of age. Average daily running speed (m/min) was calculated by dividing the daily distance by the daily duration (13,15,26). Weight of food was measured twice weekly to determine average daily food consumption. Food was manually removed from the solid surface cage floor, and every attempt was made to obtain all remaining food in the cage. Body weight was measured once weekly throughout the study period.

Food consumption and body weight were each analyzed using a Group x Time repeated measures analysis of variance (ANOVA) to determine differences between the four groups in average daily food consumption and average weekly body weight, respectively. Multivariate analyses were used to determine differences between groups at each time point. All post-hoc analyses were performed using the Games-Howell test. Running distance, duration and speed were each compared between the two running groups using a Group x Time repeated measures ANOVA to determine differences between groups across time. Multivariate analyses were used to determine differences between groups each week. The relationship between running-wheel activity and food consumption for the SWR/J runners and DBA/2J runners was analyzed using bivariate correlations for distance, duration, and speed, respectively. The alpha value was set *a priori* at 0.05 for all analyses.

Results

One mouse died from each group during the study period, with the exception of the SWR/J runner group. Additionally, the wheel activity monitoring device associated with one mouse in the SWR/J runner group malfunctioned for extended periods, so these data were not included in the analysis. Therefore, the following data represent four mice per group. SWR/J runners consumed a significantly higher amount of food (6.0 ± 0.4 g/day) compared to SWR/J non-runners (4.7 ± 0.2 g/day; $p=0.03$), DBA/2J runners (4.6 ± 0.2 g/day; $p=0.02$), and DBA/2J non-runners (4.2 ± 0.2 g/day; $p=0.006$) on average and over time (Figures 1a and 1b). SWR/J non-runners consumed a significantly higher amount of food compared to DBA/2J non-runners ($p=0.03$). There was no difference in food consumption between SWR/J non-runners and DBA/2J runners ($p>0.05$) or between DBA/2J runners and DBA/2J non-runners ($p=0.13$).

Daily distance ($p<0.001$; Figure 2a) and duration ($p<0.001$; Figure 2b) on the running wheel were significantly greater for the SWR/J runners (6.4 ± 0.7 km/day and 333.6 ± 40.5 min/day, respectively), for each week of the study period, compared to the DBA/2J runners (1.6 ± 0.4 km/day and 91.3 ± 23.0 min/day, respectively). Speed throughout the study period between SWR/J runners (19.0 ± 0.6 m/min) and DBA/2J runners (16.9 ± 1.1 m/min) was not significantly different ($p=0.07$; Figure 2c).

There was a significant correlation between average daily distance and average daily food consumption ($r=0.74$, $p<0.001$, Figure 3a), between average daily duration and average daily food consumption ($r=0.68$, $p<0.001$, Figure 3b), and between average daily speed and average daily food consumption ($r=0.58$, $p<0.001$, Figure 3c) in all mice. However, when considering the individuals strains, the relationship between running-wheel activity and food consumption was only significant for the SWR/J mice for distance and speed (Figures 3a-c).

Table 1 shows correlations between running-wheel activity and body mass and between average daily food consumption and body mass. Finally, while the SWR/J mice ate more, there was no difference in body mass between groups across time or at any time point ($p > 0.05$; Figure 4).

Discussion

The purpose of this study was to determine the effect of innate activity level and running-wheel access on food consumption in two inbred mouse strains, a high-active strain (SWR/J) and a low-active strain (DBA/2J). The data revealed significantly higher food consumption for the SWR/J runners compared to the DBA/2J runners, for the SWR/J non-runners compared to the DBA/2J non-runners, and for the SWR/J runners compared to the SWR/J non-runners (Figure 1). Additionally, there was a strong positive correlation between daily food intake and daily wheel activity, as measured by average daily distance, duration, and speed (Figure 3).

Previous data have shown that increased wheel activity is associated with increased food consumption, suggesting mice or rats that run more require higher energy intake (4,7,12,24, 25). In our study, the SWR/J runners consumed 27% more food than the SWR/J non-runners. This is similar to the 20-25% increase in food consumption found in high-active strains exposed to a functional running wheel (24). The increased energy expenditure from the wheel likely resulted in increased food consumption, as suggested by Swallow and colleagues (24). The SWR/J runners in our study consumed 30% more food than the DBA/2J runners (Figure 1), which is likely due in part to wheel activity being nearly four-fold higher in the SWR/J mice (Figure 2). Additionally, the SWR/J non-runners consumed 12% more food than the DBA/2J non-runners, which has been reported previously (2). This suggests that either SWR/J mice inherently eat more compared to DBA/2J mice, or that the SWR/J strain was more active even without a running wheel compared to the less active DBA/2J strain, resulting in greater food consumption. This is contrary to the findings of Swallow and colleagues (24) who found no difference in food consumption between high-active and control strains of mice that did not have access to a functional running wheel.

A previous study using a control strain not bred for high activity showed a 19.5% increase in food consumption with mice that had wheel access (24). In contrast, our study showed no significant difference in food consumption (less than 10%) between DBA/2J runners DBA/2J non-runners, though it is recognized that the strain used by Swallow and colleagues (24) may have been more active than the DBA/2J strain, possibly resulting in the higher food consumption in their study. We have previously shown that caloric intake of C57Bl/6 mice fed either a high-fat or high-carbohydrate diet (*ad libitum*) did not differ between mice that had access to a running wheel compared to those that did not have access to a running wheel (10). Assuming food intake is related to energy expenditure, as supported in the literature, it is possible that because the DBA/2J mice have such a low level of running-wheel activity that the DBA/2J non-runners were able to achieve a similar activity level (energy expenditure) within their cage as those with a wheel, and thus the food consumption levels were similar. Our results support previous findings which suggest that energy expenditure of wheel activity accounts for only a small percentage of the total daily energy expenditure (12) and that access to a wheel may decrease other activities that result in energy expenditure, such as climbing on the cage lid (8,21). This idea is further supported by studies showing that mice increase home-cage activity when housed without wheels (16). Thus, the DBA/2J non-runners, in the absence of wheels, possibly increased home-cage activity to similar levels of DBA/2J runners, as evidenced by similar levels of food consumption and weight gain. On the other hand, when using a prediction equation to estimate the oxygen cost of wheel-running (19), the DBA/2J runners would have expended approximately 1.78kcal/day in order to perform their running wheel activity. While daily food consumption was not significantly different between DBA/2J runners and non-runners, the DBA/2J runners consumed an average of 0.4g/day more food than the DBA/2J non-runners (Figure 1). The standard chow used in this study provided 3.1kcal/g of metabolizable energy; thus, when accounting for this additional 0.4g of food the DBA/2J runners consumed an average of 1.24kcal/day more than the DBA/2J non-runners. This additional caloric intake (1.24kcal) is similar to the caloric expenditure of the wheel

activity (1.78 kcal). Based on these values it appears the DBA/2J runners consumed a greater amount of food to support the running, though the difference was not significant.

There was no difference in body mass between the groups in our study (Figure 4), suggesting that SWR/J and DBA/2J mice may have instinctively balanced their food consumption with their energy expenditure. However, previous results are mixed as to the effect of wheel access on body mass in both male and female rodents, with some finding decreased or attenuated body mass with wheel use (3,4,17,23,25), and others finding that exercise had no effect on body mass (8,10,20). It is interesting to note that in several studies which suggested running-wheel activity decreased or attenuated weight gain, the mouse strains used tended to be highly active (3,4,23), while those that found wheel access had no effect on body mass used low-active strains (8,10). However, Swallow and colleagues (22) found access to a running wheel for seven to eight weeks did not attenuate weight gain in the high-active strain to a greater degree compared to weight gain in the controls. Similarly, our study showed the running-wheel activity affected body mass for the high-active or the low-active strains in a similar manner, suggesting the increased running-wheel activity of the high-active strain was compensated by increased food consumption, or vice-versa. However, high-active hamsters that had access to a running wheel for one year increased food consumption by the second week compared to a non-wheel group, but no difference was found in body mass between groups until the sixteenth week (6). And in this case, the wheel group was significantly heavier than the non-wheel group (6). Nehrenberg and colleagues (17) found higher wheel activity was not always associated with weight loss. They concluded that changes in body fat may not always be due to the amount of wheel activity, further suggesting the influence of genetic background (17). However, it appears the mice in the Neherenberg et al. (17) study that had greater wheel activity also ate a greater volume of food compared to those that were less active.

While there were no differences in body mass between groups, it is unclear whether there were differences in lean mass or fat mass because body composition was not measured. However, data from our lab using C57BL/6 mice showed access to a running wheel had no effect on lean body mass. Any differences in body mass between mice with access to a running wheel compared to mice without access to a running wheel were due to differences in fat mass (10). It should also be noted that SWR/J mice have been shown to be obesity-resistant (28); thus, it is possible the lack of difference in body mass between the SWR/J runners and SWR/J non-runners could be due to obesity resistance rather than increased activity due to the running wheel. However, it is equally plausible that access to the running wheel resulted in greater energy expenditure thereby balancing the increased food intake.

It is interesting to note the strong, positive relationship between body mass and average daily food intake for the DBA/2J mice (Table 1), compared to the non-significant relationship between food intake and body mass for the SWR/J mice. Additionally, in the case of the DBA/2J mice, there was no relationship between activity level and food consumption. However, there was a significant relationship between activity level and food consumption for the SWR/J mice. These data seem to support the idea that the increased food consumption in the SWR/J mice was driven by the increased running-wheel activity.

Harri and colleagues (8) found that low-active mice (~2km/day on a running wheel) exposed to a running wheel expend less time, and thus energy, in other activities (e.g. – climbing on the cage lid). Based on our finding that DBA/2J runners and non-runners had similar food consumption and body mass values, it is logical to conclude that access to a running wheel did not substantially increase the daily physical activity DBA/2J mice. This assumption seems reasonable since the DBA/2J mice averaged only ~90 minutes per day (<2km/day) on the running wheel over the duration of the study. On the other hand, SWR/J mice averaged slightly less than six hours per day (~6.5km/day) on the running wheel throughout the duration of the

study. It seems reasonable to conclude the SWR/J mice without a running wheel were unable to achieve the activity level and energy expenditure of SWR/J runners with cage activity alone. Thus, the SWR/J non-runners had the same body mass as the SWR/J runners, but they consumed significantly fewer calories.

One possible limitation to our study is the effect of differing estrous cycles in the female mice and its effect on running-wheel activity, as it is known that sex hormones have an influence on running-wheel activity (14). However, because wheel activity was recorded daily and averaged each week for 13 weeks, we feel any effect of differing estrous cycles between the strains would be dampened and would have minimal effect on the results. Additionally, because cage activity was not monitored outside of the wheel, it is difficult to estimate total energy expenditure. Finally, Koteja et al (11) have suggested that food wastage should be considered when calculating food consumption. While every attempt was made to measure all of the food remaining in the cage, we recognize that there was a possibility of error by missing small pellets. Nonetheless, the average variance in measured food consumed between animals was very small ($SE \pm 0.2g$ for each strain).

In conclusion, our findings suggest that, at least during a 13-week trial early in the lifespan, SWR/J and DBA/2J mice tended to balance energy intake with energy expenditure. However, increased running-wheel activity in mice was associated with increased food consumption only in the SWR/J mice. There was no difference in body mass between any of the groups despite access to a running wheel and genetic differences in activity level. Food consumption of a high-active mouse strain (SWR/J) with a running wheel was increased above that of a high-active control, likely due to the increased activity level on the wheel, resulting in similar weight gain compared to control mice. However, in a low-active strain (DBA/2J) the addition of a running wheel did not result in significantly increased food consumption, suggesting energy expenditure of cage activity in the control DBA/2J mice was similar to the energy expenditure of the wheel activity since body mass was similar between the two groups. Finally, the high activity of the SWR/J mice was associated with greater food intake compared to the DBA/2J mice in both the running wheel and control setting.

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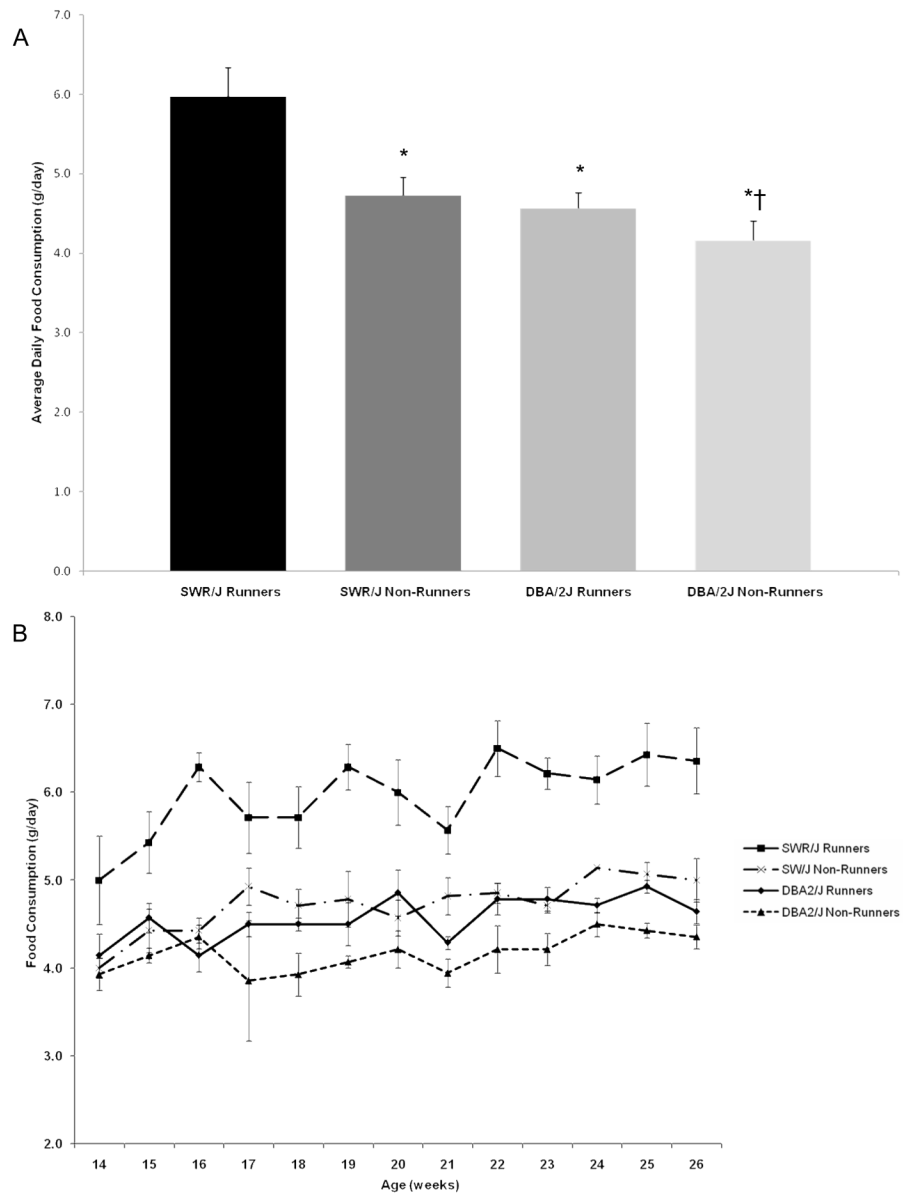
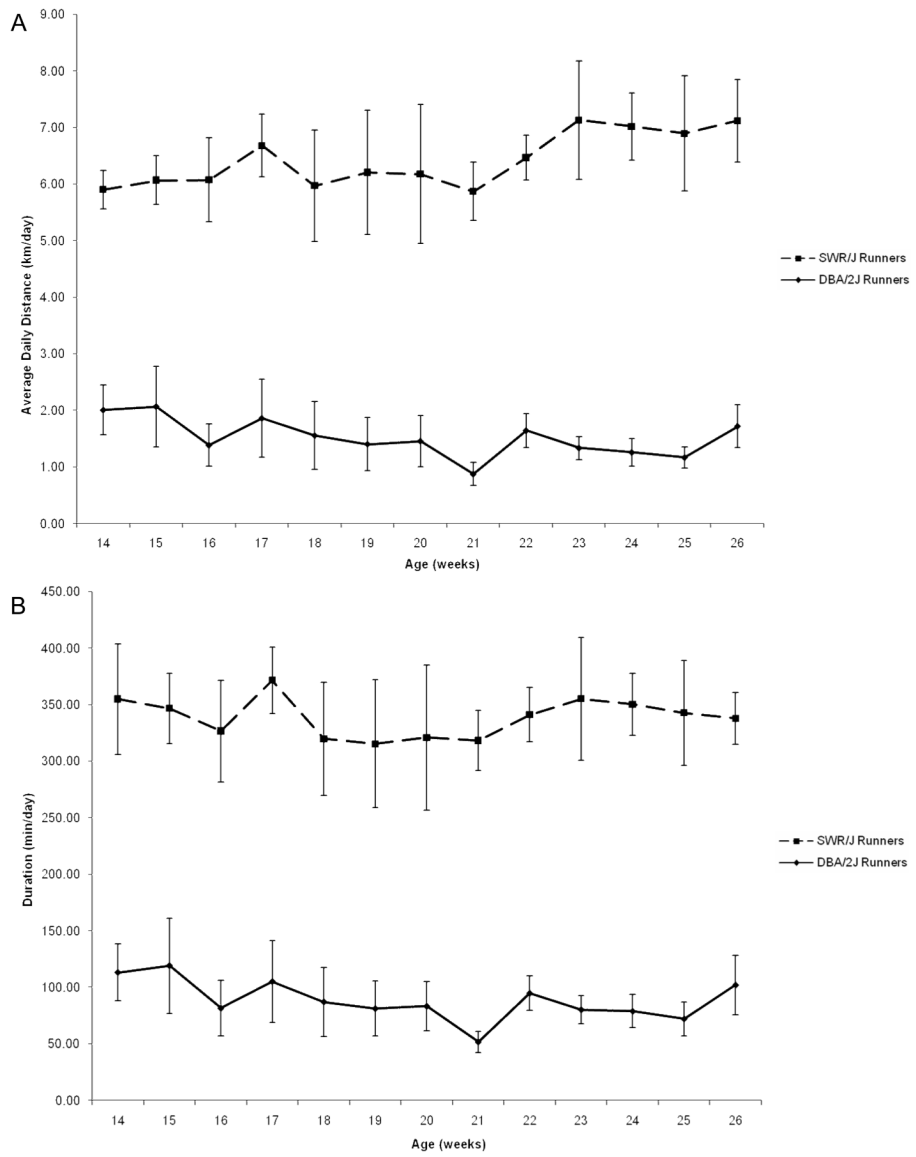


FIGURE 1. Average daily food consumption (mean±SE) overall (A) and at each week (B) for all groups. *significantly different from SWR/J Runners ($p<0.05$); †significantly different from SWR/J Non-Runners ($p<0.05$).



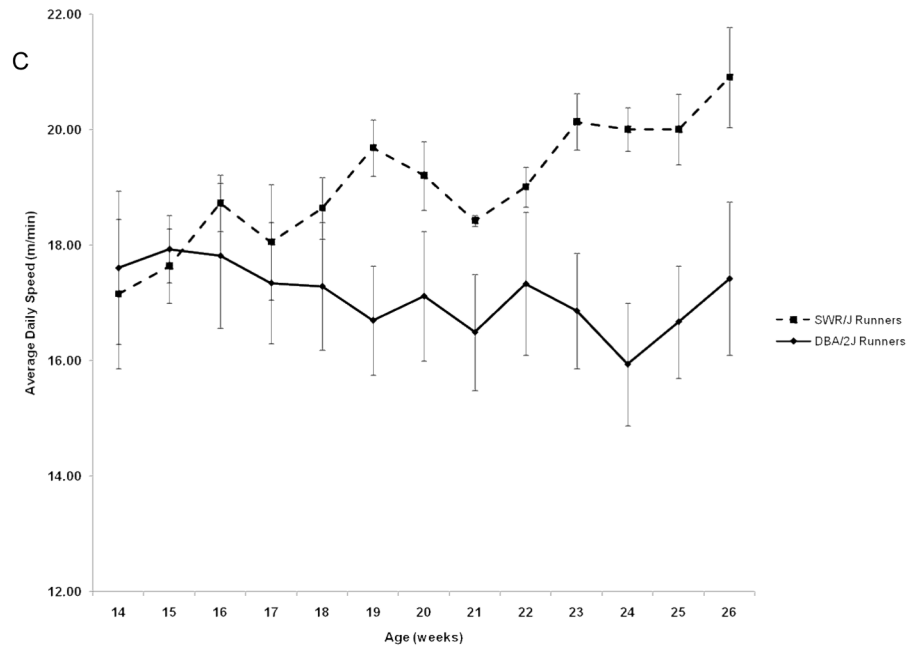
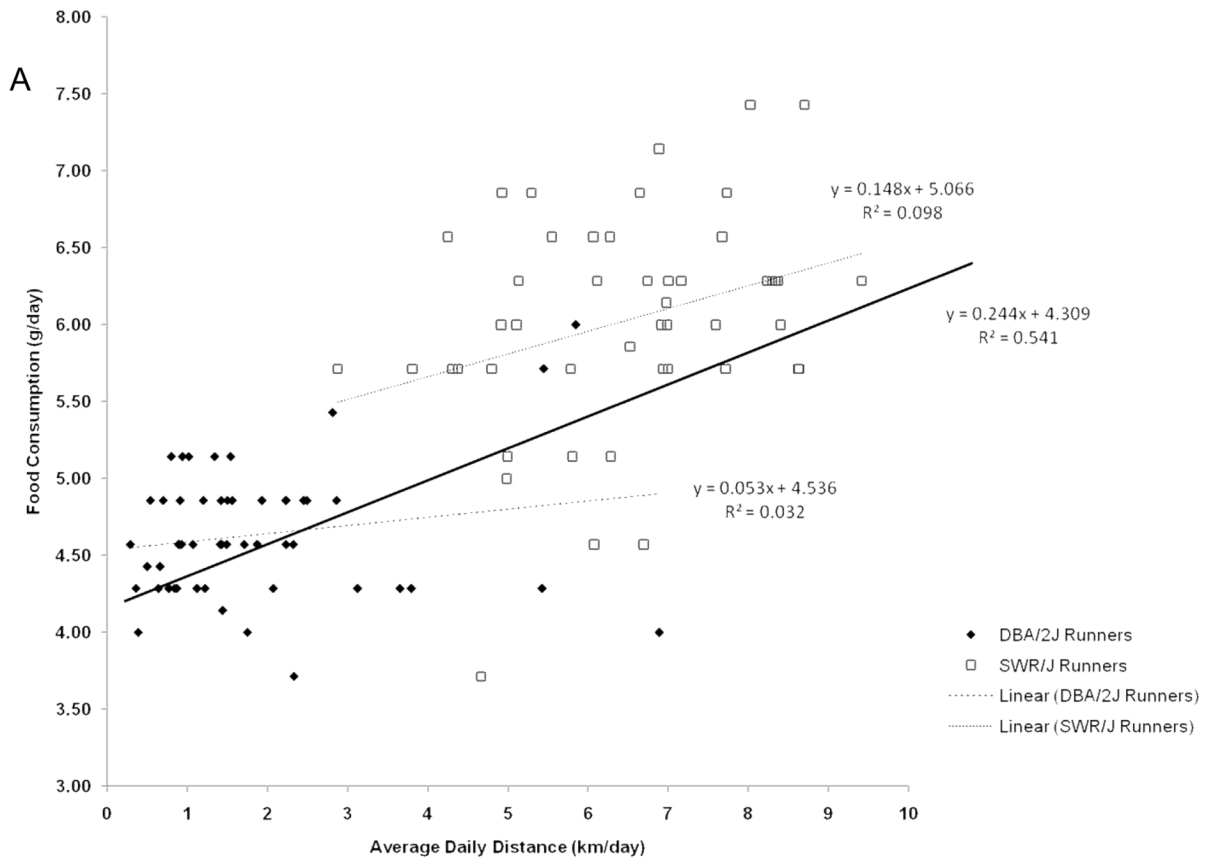


FIGURE 2. Average daily distance (A), duration (B), and speed (C) on a running wheel for each group (mean \pm SE). SWR/J Runners significantly greater than DBA/2J Runners for distance and duration ($p<0.05$) but not for speed ($p=0.07$).



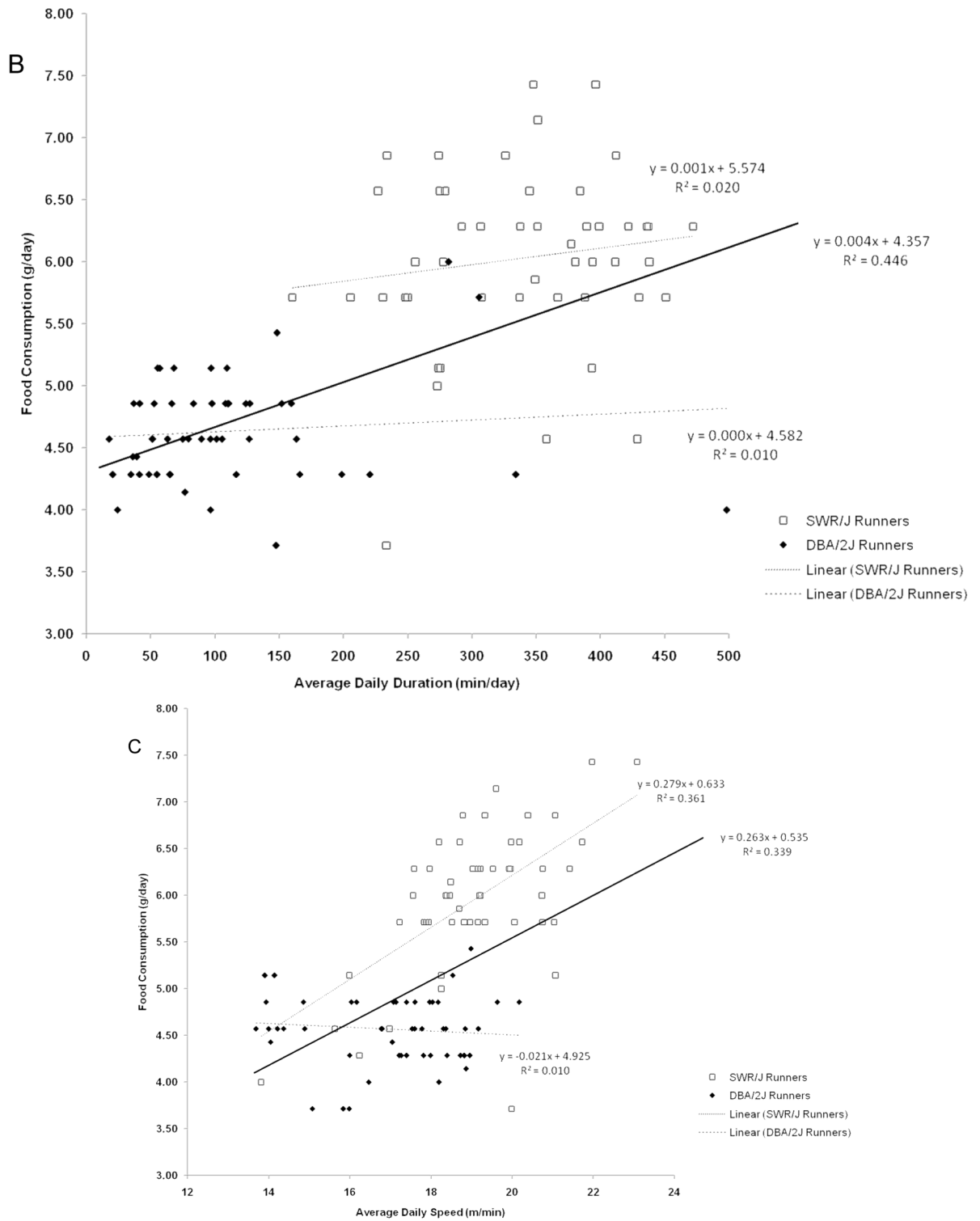


FIGURE 3. Relationship between average daily food consumption and average daily distance (A), average food consumption and average daily duration (B), and average food consumption and average

daily speed (C). Each data point represents one mouse for one week; thus, each mouse is represented 13 times in each figure. Solid lines represent all mice combined.

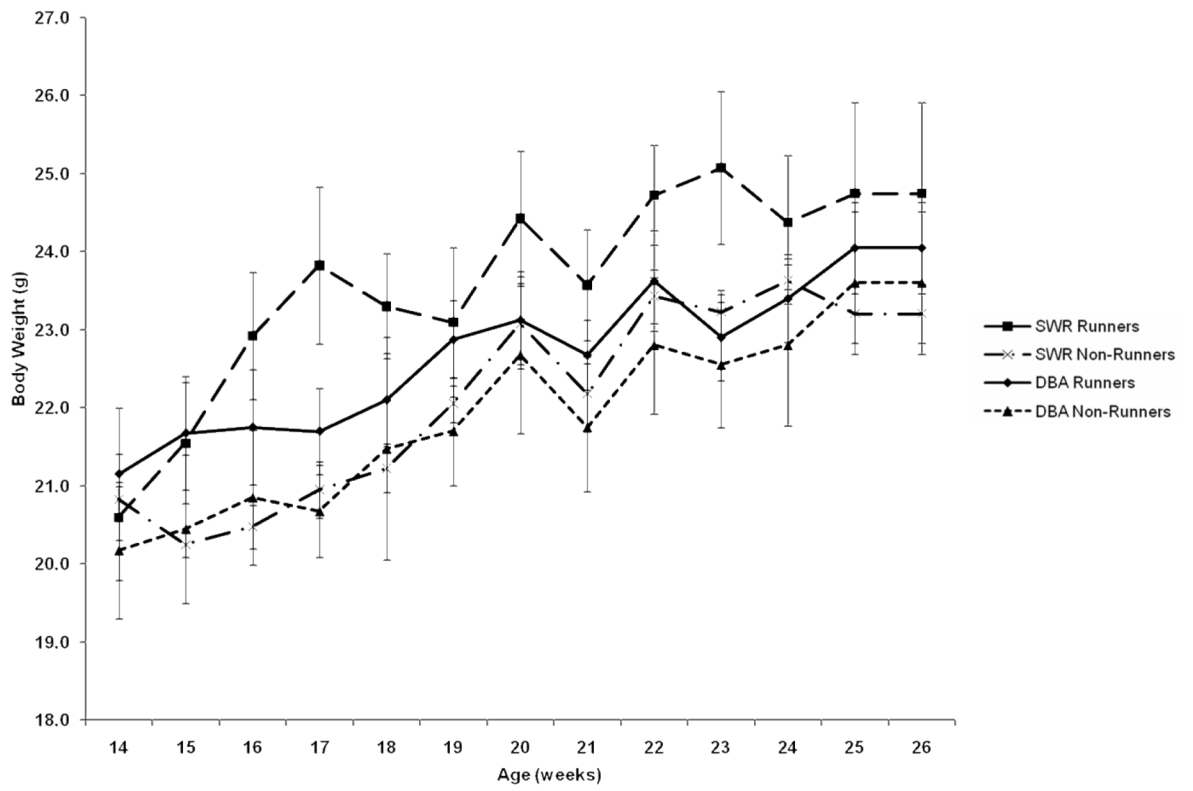


FIGURE 4. Average body mass over the 13-week period (mean±SE). No difference between groups ($p>0.05$).

TABLE 1

Relationship between body mass, running wheel activity and food consumption

	DBA/2J Body Mass	SWR/J Body Mass	Combined Body Mass
Avg. Distance	0.02	0.48**	-0.05
Avg. Duration	0.08	0.41**	-0.06
Avg. Speed	-0.28*	0.10	-0.17
Food Consumption	0.70**	0.13	0.01

Values represent Pearson's r.

DBA/2J (N=4), SWR/J (N=4), Combined (N=8). Each week a daily average was calculated for running wheel activity and food consumption, while body mass was measured once weekly. Correlations shown above were calculated using each of the weekly values for distance, duration, speed, food consumption, and body mass for each mouse through the 13-week study period.

*
p<0.05

**
p<0.01