

# Individual Variation in Locomotor Behavior and Maximal Oxygen Consumption in Mice

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FRIEDMAN, W. A., T. GARLAND, JR. AND M. R. DOHM. *Individual variation in locomotor behavior and maximal oxygen consumption in mice.* PHYSIOL BEHAV 52(1) 97-104, 1992.—Individual differences in open-field activity and emotionality (number of defecations and urinations), voluntary wheel running, voluntary and forced maximal sprint running speed on a photocell-timed racetrack, swimming endurance, and maximal oxygen consumption ( $\dot{V}_{O_2max}$ ) were studied in 35 random bred male ICR mice. With the exception of latency in the open field and voluntary speed on a racetrack, all measurements were significantly repeatable on two successive trial days. Maximal oxygen consumption (corrected for body size) was positively correlated with amount of wheel running during each day of a 7-day test, and the correlation became stronger throughout the testing period; however, none of the daily correlations reached statistical significance. The first factor from a principal components (PC) analysis showed positive loadings (component correlations) for all measures of speed in the open field, for both voluntary and forced maximal speeds on the racetrack, and for  $\dot{V}_{O_2max}$ , but a negative loading for emotionality. Wheel running and  $\dot{V}_{O_2max}$  loaded positively on PC 2. Only swimming endurance loaded strongly on PC 3; this trait was uncorrelated with any other measure of physiology or behavior. These results suggest that measures of both voluntary and forced locomotor speed, as well as amount of voluntary wheel running, may be related to aerobic physiological capacities in untrained mice.

Ambulation	Emotionality	Exercise	Locomotion	Open-field test	Oxygen consumption
Swimming endurance		Wheel running			

THE biological importance of individual variation has recently been reemphasized in the fields of behavior and comparative physiology [e.g., (3,6,32,43)]. An appreciation of the fundamental importance of individual variation is not, however, new to these and related fields [e.g., (19,38,46)]. For example, Tryon (42) outlined four main problems that should be addressed when studying individual variation:

1. How consistently individuals vary from one another and how constant these variations are;
2. the degree to which individual variation in one behavioral domain correlates with individual variation in other types of behavior;
3. the extent to which physiology and morphology relate to individual variation in behavior; and
4. the relationship between individual variation and heredity.

Operationally, individual differences can be documented by measuring each of a series of individuals' multiple times and testing for significant repeatability, defined herein as the simple Pearson product-moment correlation between scores in tests on successive days.

Rodents have been the subject of many studies of individual behavioral variation, and aspects of locomotor behavior are commonly studied by psychologists and neurobiologists. Locomotor behavior is also of interest to comparative physiologists, physiological ecologists, and ethologists, because of its ob-

vious potential relevance for animals living in the wild (3,11,14,17,27,43). Abilities to perform various types of locomotion are thought to be of key importance in a variety of natural situations, such as capturing prey or escaping from predators [e.g., (3,11,17,27)]. For example, Wilcox (45) suggests that the ability to escape from water may be important for Darwinian fitness in free-living *Rattus norvegicus*.

Two of the most common measures of locomotor behavior in rodents are voluntary wheel running [e.g., (13,28,29)] and open-field behavior [e.g., (1,8,13,20,40,41,44)]. Numerous studies have focused on the heritability of individual differences in locomotor behavior (8), and both wheel running and open-field activity are heritable within various strains of rodents [(33,35), references therein]. Relatively few studies, however, have documented correlations between different measures of locomotor behavior at the level of individual variation (32), although a number have examined aspects of locomotor behavior in several inbred lines, and sometimes their crosses, or in lines of mice selected for open-field activity [(8,10,13,24,35,40), see also (26)]. Surprisingly few studies have addressed the extent to which locomotor behavior correlates with variation in physiological traits [but see (20,21,26), references in (44)], such as muscle contractile properties or maximal oxygen consumption (see below), or even body size (41). Thus, the degree to which individual differences in locomotor behavior reflect physiological capacities for exercise remains unknown for rodents. In contrast, a number of studies

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TABLE 1  
DESCRIPTIVE STATISTICS FOR VARIOUS MEASURES OF LOCOMOTOR BEHAVIOR AND PERFORMANCE

Behavior or Performance	Units	Mean	SE	CV%	Min	Max
Open-field defecations + urinations, trial 1	Number	4.53	0.541	69.7	0	14
Open-field defecations + urinations, trial 2	Number	4.88	0.444	53.1	1	13
Mean defecations + urinations	Number	4.71	0.403	50.0	0.5	11
Open-field latency, trial 1	s	14.1	5.82	241.4	1.0	203.7
Open-field latency, trial 2	s	3.4	1.07	183.9	0.5	36.1
Lower latency	s	2.5	0.42	98.6	0.5	14.4
Open-field mean speed, trial 1	m/s	0.10	0.005	28.6	0.02	0.15
Open-field mean speed, trial 2	m/s	0.08	0.005	33.3	0.03	0.15
Higher mean speed	m/s	0.10	0.004	24.8	0.03	0.15
Open-field maximum speed, trial 1	m/s	0.38	0.010	15.7	0.14	0.48
Open-field maximum speed, trial 2	m/s	0.41	0.007	10.1	0.25	0.46
Higher maximum speed, trial 1	m/s	0.41	0.007	10.7	0.25	0.48
Open-field SD of speed, trial 1	m/s	0.084	0.003	19.0	0.025	0.103
Open-field SD of speed, trial 2	m/s	0.089	0.002	14.6	0.041	0.089
Mean SD of speed	m/s	0.087	0.002	14.9	0.033	0.104
Voluntary speed over 5.5 m, trial 1	m/s	0.09	0.010	64.1	0.01	0.20
Voluntary speed over 5.5 m, trial 2	m/s	0.20	0.019	56.4	0.03	0.50
Higher voluntary speed	m/s	0.21	0.019	53.4	0.03	0.50
Forced sprint speed, trial 1	m/s	0.97	0.035	21.2	0.64	1.52
Forced sprint speed, trial 2	m/s	1.11	0.038	20.2	0.62	1.65
Higher sprint speed	m/s	1.13	0.035	18.4	0.71	1.65
Swimming endurance, trial 1	min	3.13	0.424	80.3	0.43	10.6
Swimming endurance, trial 2	min	5.59	1.521	161.1	0.63	54.9
Higher endurance	min	5.89	1.516	152.3	1.33	54.9
Wheel running, day 1	revs	2,591.0	287.26	64.6	12	6,608
Wheel running, day 7	revs	3,744.2	475.04	72.9	24	13,764
$\dot{V}_{O_2}$ max, trial 1	ml $O_2$ /h	345.2	4.25	7.3	307.5	415.5
$\dot{V}_{O_2}$ max, trial 2	ml $O_2$ /h	348.9	4.82	8.2	298.2	407.6
Higher $\dot{V}_{O_2}$ max	ml $O_2$ /h	347.0	4.74	8.1	297.8	404.6
Body mass at higher $\dot{V}_{O_2}$ max	g	38.7	0.64	9.8	32.4	47.6

correlating locomotor behavior with individual variation in physiology have been done with reptiles [e.g., (14,15), review in (17)].

The purposes of the present study were three-fold: 1) to quantify the extent and repeatability of individual differences in several measures of locomotor behavior and physiological performance, 2) to test for correlations between the various measures, and 3) to determine whether any measure of locomotor behavior was significantly correlated with maximal oxygen consumption ( $\dot{V}_{O_2}$ max). Maximal oxygen consumption sets an upper limit to the intensity of activity that can be sustained aerobically, without accumulating an oxygen debt, which leads ultimately to fatigue. Mammals exercising at or above the speed at which  $\dot{V}_{O_2}$ max is attained tire quickly, within minutes, whereas those exercising at lower speeds can sustain activity for long periods of times, sometimes for hours (5). The  $\dot{V}_{O_2}$ max is also considered to represent perhaps the best single indicator of organismal aerobic capacity and overall cardiovascular fitness (2,23,37). Work in progress in our laboratory will examine the heritability of  $\dot{V}_{O_2}$ max [cf. (4,15)] and selected locomotor behaviors in this same strain of mice [see also (25)].

Our measures of locomotor behavior ranged from low to high in terms of the demands placed on an animal's aerobic capacities. Open-field activity, for example, occurs at relatively low speeds and constitutes a low work load; thus, this behavior would not be expected to be limited by aerobic capacities. Voluntary wheel running, on the other hand, may occur at levels

high enough to tax an individual's aerobic capacities, and might correlate positively with  $\dot{V}_{O_2}$ max. We also made several measures of locomotor performance (3,17) under forced conditions, including both maximal sprint running speed and swimming endurance, in an attempt to link physiological and behavioral variation. Because different measures of locomotor behavior and performance may depend partly on common physiological support systems, we hypothesized positive correlations between measures of mean and maximum speed in the open field, voluntary and forced maximum speed in a racetrack, swimming endurance, and amount of voluntary wheel running. We also hypothesized that  $\dot{V}_{O_2}$ max would correlate more strongly with measures of sustained locomotor activity (swimming endurance, voluntary wheel running) than with forced sprint speed.

#### METHOD

##### Animals

We studied 35 male mice of the random bred ICR strain, born 7–15 April 1989 and tested 18 July to 24 August 1989. These individuals represented sets of 1–8 siblings ( $\bar{x} = 3.5$ ) from 10 families. Parents (each individual from separate litters) of the subject mice were obtained at 3 weeks of age from Harlan Sprague-Dawley (Indianapolis, IN, Building 202, Barrier A) and bred at 45 days of age. All individuals were toe-clipped for individual identification at birth and again at 2 weeks. No more than two toes per foot were clipped; such toe-clipping does not affect performance in these mice (unpublished data). After

TABLE 2  
 PAIRED *t*-TESTS COMPARING REPLICATE TRIALS

Behavior or Performance	Transformation	Pearson's <i>r</i>	Significance	<i>t</i> *	Significance
Open-field defecations + urinations [34]	Square root	0.355	0.039	0.99	0.330
Open-field latency [34]	log	0.289	0.098	-7.86	<0.001
Open-field mean speed [34]		0.692†	<0.001	-3.56	0.001
Open-field maximum speed [34]	Cubed	0.625	<0.001	3.23	0.003
Open-field SD of speed [34]	Cubed	0.401‡	0.019	1.79	0.083
Voluntary 5.5 m speed [35]		0.196	0.260	5.57	<0.001
Forced sprint speed [35]		0.711	<0.001	5.08	<0.001
Swimming endurance [35]	log	0.584	<0.001	3.44	0.002
Wheel running, days 1-2 [34, 28]		0.734	<0.001	-1.90	0.068
Wheel running, days 6-7 [34, 33]		0.646§	<0.001	-1.49	0.147
$\dot{V}_{O_2\max}$ [35]	log	0.809	<0.001	1.20	0.240
Body mass at $\dot{V}_{O_2\max}$ [35]		0.983	<0.001	-1.51	0.139

Number of subjects shown in brackets.

\* Positive value indicates second trial higher than first.

† Deleting one individual (#537) yields  $r = 0.823$ .

‡ Deleting one individual (#537) yields  $r = 0.668$ .

§ Deleting one individual (#520; 4,433 revolutions on day 6 vs. 13,764 on day 7) yields  $r = 0.852$ .

weaning at 19 days of age, individuals were housed in same-sex groups of four per cage. Cages (27 × 17 × 12.5 cm deep) were made of clear plastic with metal or wire tops. Food (Purina Rodent Chow, High-energy Formula) and water were available ad lib. Photoperiod was 12:12 light:dark, centered at 1300 h, and temperature was approximately 21 °C throughout the testing period.

### Procedure

Animals were tested twice, on consecutive days, for each behavior, with tests given in the following order: voluntary running speed, forced maximal sprint running speed, maximal oxygen consumption, swimming endurance, voluntary wheel running, open-field activity. This sequence of testing was chosen so as to begin and end with measures of voluntary activity while simultaneously minimizing the time between them and the (more physiological) tests of forced aerobic capacity and swimming endurance. Below, we discuss the tests in a different order, proceeding from putatively less to more aerobic.

All testing was done during the photophase, between 1100 and 1900 h. Animals were weighed after each testing period, with the exception of wheel running. A random numbers program was used to determine the testing order of individuals for voluntary activity, sprint speed, and  $\dot{V}_{O_2\max}$ ; for other measures, testing order was arbitrary. A single experimenter conducted each test, with the exception of swimming endurance, which involved all three authors simultaneously.

**Open-field activity.** A 100 × 100 cm open arena with 45-cm walls was used. The arena was constructed from four metal walls painted black and a floor made from two equally sized Plexiglas sheets covered with matte-black polyethylene strips. A video camera was placed 245 cm above the arena to record trials. Each animal was placed by hand into the middle of the arena, facing the same direction, and filmed for 15 min. We used an open-field test of 15-min duration because activity over this length of time is more likely to depend in part on aerobic capacity than is a test of shorter duration [e.g., 3 min in (8); 4 min in (24); review in (44)]. At the end of each trial, the numbers of fecal pellets and urine pools were counted. (Analyses using only the number of defecations yielded similar results.) The arena was cleaned with a wet sponge after each run.

Video analysis was done using ExpertVision software version 1.1 (Motion Analysis Corporation, Santa Rosa, CA) on a Sun Microsystems workstation. Tapes were viewed with a Panasonic video monitor and video cassette recorder AG-6300. Fifteen min of video were digitized at one frame/second, video analysis beginning immediately after the observer's hand left the arena. The mouse's location (centroid) was computed for each of the 900 video frames, thus allowing computation of the distance moved at 1-s intervals. We then recorded the mean velocity, maximum velocity, and standard deviation of velocity for each 15-min trial. Mean velocity, multiplied by 900 s, yields total distance moved. We were particularly interested in whether maximum velocity might correlate with forced sprint speed. In addition, movement latency was recorded as the amount of time elapsed before each subject's nose first touched a wall. Latency was measured to the nearest 0.1 s by an observer viewing each taped trial.

**Voluntary running speed.** Activity was measured as the time taken to traverse 5.5 m of an 8-m long by 16.5-cm wide photocell-timed racetrack, with short-pile artificial grass substrate (11). Each mouse was placed at the start of the racetrack in the 38-cm area before the first photocell, then allowed to cover the length of the track without interference from the observer. Actual timing was done with a stopwatch, as the first and last photocells were crossed (5.5 m).

**Maximal sprint running speed.** Maximal sprint speed was measured with standard techniques on the racetrack described above. Each subject was timed, with the use of the photocells, while chased along the track with a padded meter stick as fast as it would run (11). Twelve sets of photocells spaced at 0.5-m intervals were interfaced to a microcomputer that recorded all time intervals. After each run, subjects were prodded to walk slowly back to the start to minimize handling stress. Subjects were run five times in quick succession on each trial day and the maximum speed for each day was taken as the fastest 1.0-m interval (three consecutive photocells) recorded. Both values were analyzed for repeatability; higher values were used in other analyses because maximal performances are more likely to reflect underlying morphological or physiological variation (14,16,17).

**Swimming endurance.** Swimming endurance capacity was measured following standard protocols [e.g., (22,31), review in

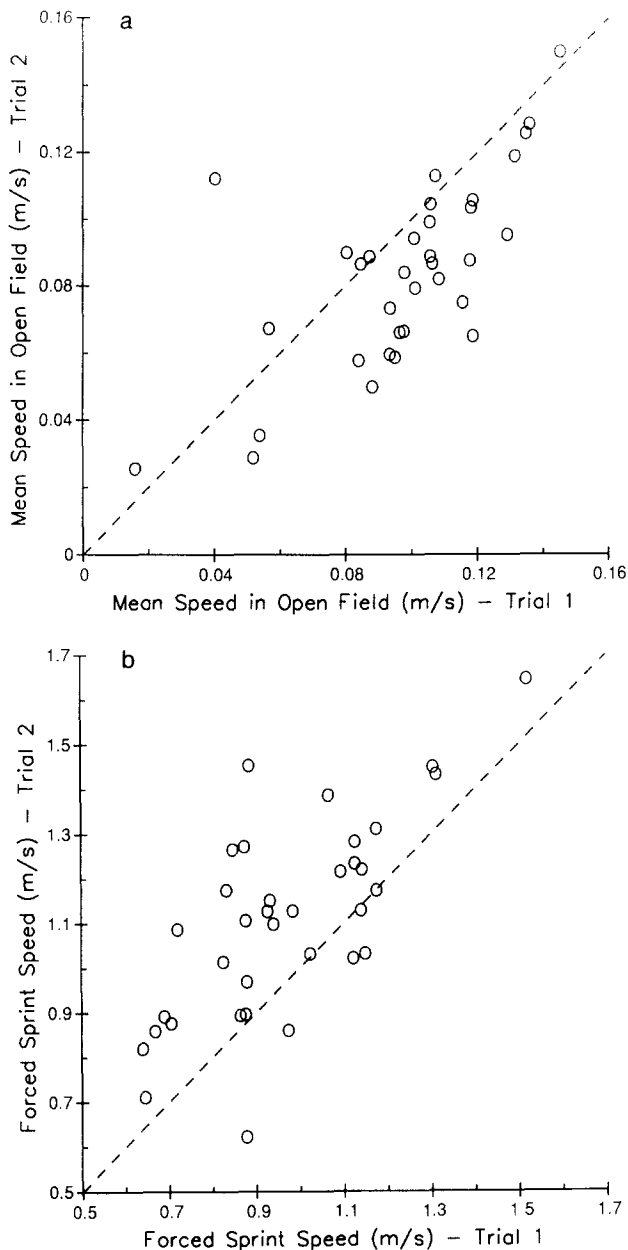


FIG. 1. Repeatability of (a) mean speed during 15-min open-field tests and of (b) maximum forced sprint speed in a photocell-timed racetrack. Dashed lines represent lines of identity (perfect repeatability). Mean open-field speed is lower on the second trial, whereas forced sprint speed is higher on the second trial (Table 2).

(7), references in (23)]. A swimming protocol was employed because preliminary studies with endurance tests on a motorized treadmill produced inconsistent results [cf. (2,12)]. Testing was done over 3 days, the first consisting of a 10-min training swim without weights followed on the second and third days by the actual endurance tests. Subjects were rinsed in a detergent solution (Ivory<sup>R</sup> liquid) to prevent air bubbles clinging to fur (7) and a 0.9 g weight was attached to their tails using a plastic paper clip. Mice were swum in plastic buckets (15.1 liter capacity; water depth approximately 30 cm) containing water at approximately 30°C, the temperature that yields highest swimming times [(7), unpublished data]. (Both initial and final water tem-

peratures were recorded for use as covariates in analyses, but neither was statistically significant.) Endurance was measured as the amount of time each animal was able to sustain itself above water. Subjects were removed when they became completely submerged for 8 s and were unable to return to the surface (7). Endurance times for the 2 days were analyzed for repeatability, whereas higher values were used in subsequent analyses.

**Voluntary wheel running.** Seventeen Wahmann activity wheels (35.5-cm diameter, 11.5-cm wide) with attached wire cages were used. Wheel activity was recorded for 7 days, measured as the number of complete rotations recorded by automatic counters. Data were collected every twenty-four h. Food and water were provided ad lib. Some individuals moved food pellets into running wheels, thus obstructing them and leading to missing data for a few days.

**Maximal oxygen consumption.** The maximal rate of organismal oxygen consumption ( $\dot{V}_{O_2,max}$ ) was measured on a motorized treadmill by using a stepped series of increasing speeds (2.5,14,25). A mouse was placed in a small chamber held just above the surface of the treadmill belt, which was moving at an initial speed of 1.0 km/h. Speed was increased by 0.5 km/h every 2 min to a maximum of 4.5 km/h or until an individual could not keep pace with the moving belt. Manual prodding and an electrical stimulating grid at the rear of the belt provided motivation. Measurement was terminated when the mouse was unable to maintain pace with the moving belt. Oxygen consumption generally increased with increasing treadmill speed, and the highest 1-min period of oxygen consumption during any run was taken as the  $\dot{V}_{O_2,max}$ , consistent with previous studies. Final treadmill speeds were always sufficient to induce exhaustion if maintained, and oxygen consumption had usually begun to decrease before a trial was ended. The  $\dot{V}_{O_2,max}$  by these techniques is highly repeatable in rats [e.g., (21)] and in ICR mice [(25), unpublished data].

An open-flow respirometry system was used. Air was drawn into the chamber through small gaps at its rear and from under its base, which rested just above the tread belt (the mice did not wear masks). Air exited the chamber via a series of small tubes in its sliding top, passed through Drierite and Ascarite columns for removal of water vapor and CO<sub>2</sub>, respectively, and then entered a thermal mass flow controller (Sierra Instruments, Inc., Monterey, CA, Side=Track Model 844). A flow rate of 2.5 SLM (from a vacuum pump downstream of the flow controller) ensured rapid chamber washout. Oxygen concentration in the excurrent air was sampled every second by an Applied Electrochemistry S-3A/II oxygen analyzer interfaced to an analog-to-digital converter and a computer. Wither's (47) equation 4a was used for computations. We also computed instantaneous values for  $\dot{V}_{O_2,max}$ , by adjusting for chamber washout times (chamber effective volume was 540 ml) [see (25)]. Instantaneous values averaged only 3.8% higher than did steady-state values, and the two measures were highly correlated ( $r = 0.976$  on trial 1 and  $r = 0.971$  on trial 2). Instantaneous values were less repeatable, however, and showed somewhat lower correlations with the behavioral traits; accordingly, we present only the results for calculations of steady-state  $\dot{V}_{O_2,max}$ .

#### Data Analysis

Several variables were transformed to improve normality. Repeatability was assessed using the interclass correlation coefficient, since several behaviors showed significant changes in mean value between replicate trials (43). All statistical analyses were performed using SPSS/PC+ version 3.0.

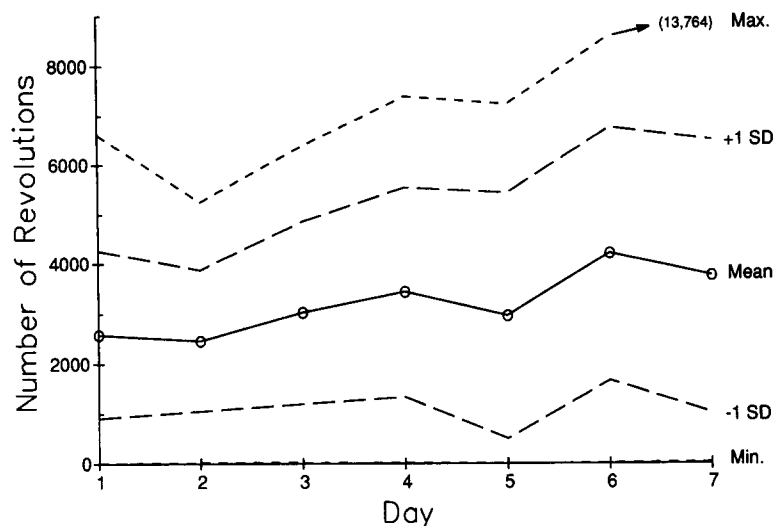


FIG. 2. Increase in amount of voluntary wheel running over 7 consecutive trial days. The overall trend is significantly positive, but number of revolutions on days 1 and 2, and on days 6 and 7, do not differ significantly (see text). The minimum number of revolutions run ranged from three to 25, whereas the maximum ranged from 5,252 to 13,764.

## RESULTS

### Variation and Repeatability

Descriptive statistics for all behavioral and physiological measurements are presented in Table 1, repeatabilities in Table 2. Nine of the 11 traits were significantly repeatable from trial to trial, the exceptions being voluntary speed over 5.5 m on the racetrack and latency in the open field. For three characters, excluding one atypical individual from the analysis yielded considerably higher repeatabilities (see Table 1 footnotes). Figure 1 shows repeatabilities for mean speed in the open field and for forced maximal speed on the racetrack.

Several traits showed changes in mean between trials. For example, both of the nonrepeatable behaviors (open-field latency and voluntary speed over 5.5 m) showed large differences between trials; mice exhibited latencies that were almost five-fold shorter during the second open-field test, and ran voluntarily

more than twice as fast on the second trial. Similarly, both maximum speed in the open field and forced sprint speed (Fig. 1b) were higher on the second trial. In contrast, mean speed in the open field was lower on the second trial (Fig. 1a).

Considering the foregoing repeatabilities and our primary goal of testing for correlations between putatively behavioral and physiological measures of locomotor capacities, we subsequently analyzed the higher of the two replicate values for all speeds, the lower open-field latency (corresponding to a higher speed when moving to the wall), the higher swimming endurance time, and the higher  $\dot{V}_{O_2\max}$ .

Voluntary wheel running tended to increase across the seven trial days (Fig. 2). Because higher amounts of activity should be more strongly related to aerobic capacity, we analyzed amount of wheel running on days 1 and 7 as separate variables. Amount of running on days 1 and 2, as well as on days 6 and 7, did not differ significantly, and both were repeatable (Table 2).

TABLE 3  
PAIRWISE PEARSON PRODUCT-MOMENT CORRELATION COEFFICIENTS

	Open-Field Behavior					Voluntary 5.5 m Speed	Forced Sprint Speed	Swimming Endurance	Wheel Running	
	Defecat.	Latency	Mean Speed	Max Speed	SD Speed				Day 1	Day 7
Open-field defecations	1									
Open-field latency	0.232	1								
Open-field mean speed	-0.519*	-0.256	1							
Open-field maximum speed	-0.510*	-0.248	0.482*	1						
Open-field SD of speed	-0.476*	-0.353	0.799*	0.683*	1					
Voluntary 5.5 m speed	-0.267	-0.114	0.322	0.587*	0.414	1				
Forced sprint speed	-0.227	-0.263	0.009	0.467*	0.300	0.412	1			
Swimming endurance	0.135	-0.195	0.054	-0.129	0.028	0.019	-0.133	1		
Wheel running, day 1	0.028	-0.014	0.016	-0.072	-0.069	0.146	0.024	-0.026	1	
Wheel running, day 7	0.021	0.038	-0.025	0.206	0.108	0.447*	0.188	0.070	0.387	1
$\dot{V}_{O_2\max}$ residual	-0.003	-0.200	0.060	0.441*	0.274	0.280	0.524*	-0.103	0.151	0.381

\* Pairwise  $p < 0.01$ .

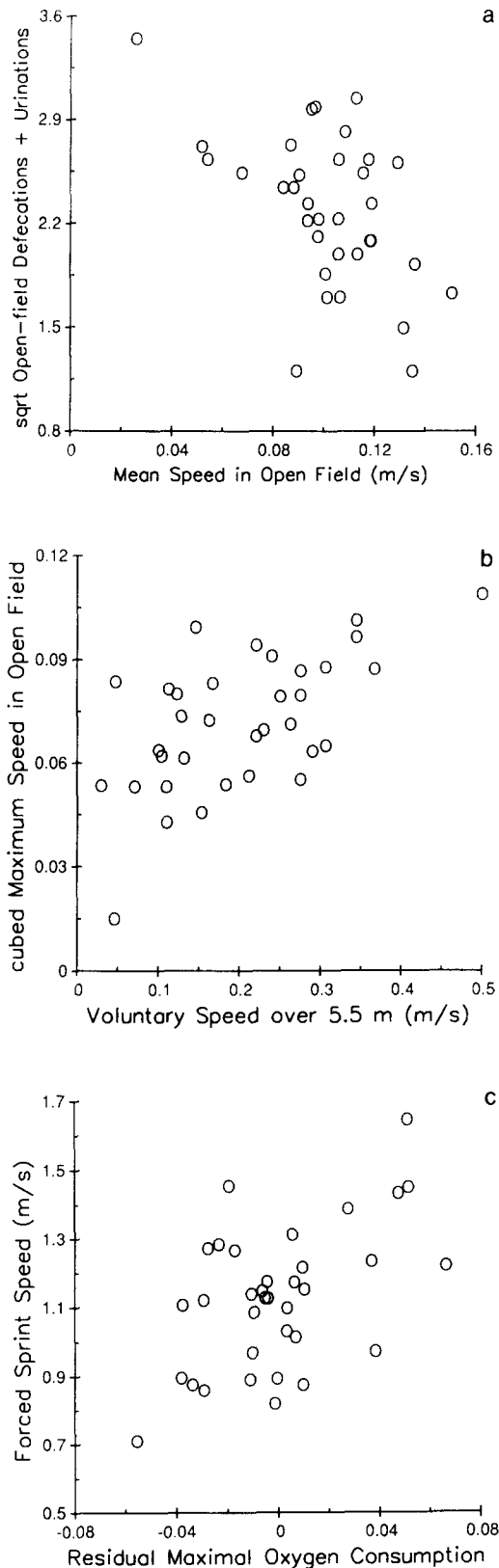


FIG. 3. Scatterplots of correlations (Table 3) between (a) the square root of the number of defecations + urinations and mean open-field speed, (b) cubed maximum voluntary speed in the open field and voluntary speed in a 5.5-m racetrack, and (c) maximum forced sprint speed and mass-corrected  $\dot{V}_{O_2\max}$ .

### Correlations

Body mass was not significantly correlated with any variable except maximal oxygen consumption (as expected, larger mice consumed more oxygen). For  $\dot{V}_{O_2\max}$ , we therefore computed residuals from log-log regressions on body mass and used these in all subsequent analyses.

Bivariate correlations are presented in Table 3. Numbers of defecations plus urinations correlated negatively with all three measures of speed in the open field (Fig. 3a), which were themselves positively intercorrelated. Voluntary speed over 5.5 m showed a significantly positive correlation with wheel running on day 7 and with maximum speed in the open field (Fig. 3b). Maximum speed in the open field and forced sprint speed both showed significantly positive correlations with residual  $\dot{V}_{O_2\max}$  (Fig. 3c) as well as with each other. Contrary to our expectations, swimming endurance did not correlate significantly with  $\dot{V}_{O_2\max}$ .

Residual maximal oxygen consumption was positively correlated with amount of wheel running on each trial day (Fig. 4), and the correlation became stronger over time as the amount of wheel running increased (Fig. 2). However, none of the daily correlations reached statistical significance (Table 3).

Principal components analysis (Table 4) yielded a first factor with strong positive loadings for all three measures of speed in the open field, as well as for both voluntary speed over 5.5 m and forced spring speed; in addition,  $\dot{V}_{O_2\max}$  showed a positive loading and open-field defecations showed a negative loading. The second principal component reflects the positive association between amount of wheel running and  $\dot{V}_{O_2\max}$ . Only swimming endurance loads strongly on PC 3, reflecting its lack of correlation (Table 3) with any other measured variable. Principal components 4 and 5 show positive loadings for open-field latency. Principal component 5 also shows a strong negative loading for amount of wheel running on day 1; thus, mice with long latencies in the open field tend to run little in wheels on the first day of exposure.

### DISCUSSION

Consistent with many previous studies [e.g., (1,10,26,35)], numbers of defecations and urinations in the open field [often interpreted as an index of emotionality (1,44)] correlated neg-

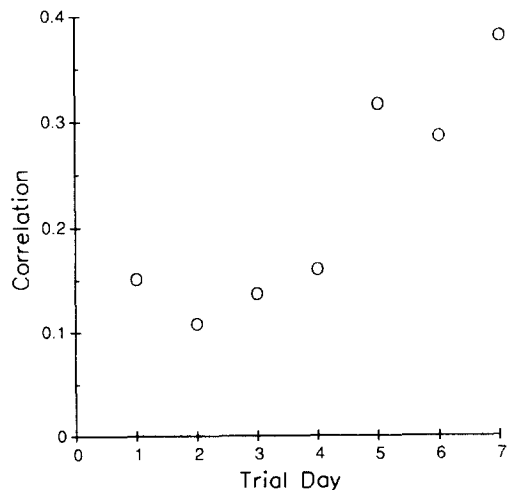


FIG. 4. Temporal increase in the Pearson product-moment correlation coefficient between amount of voluntary wheel running and mass-corrected  $\dot{V}_{O_2\max}$ , measured before exposure to activity wheels.

TABLE 4  
PRINCIPAL COMPONENTS ANALYSIS OF CORRELATION MATRIX

	PC 1	PC 2	PC 3	PC 4	PC 5
Open-field defecations	-0.606*	0.405	0.098	-0.263	0.196
Open-field latency	-0.429	0.180	-0.209	0.614*	0.460*
Open-field mean speed	0.665*	-0.507*	0.278	0.247	-0.053
Open-field maximum speed	0.865*	-0.034	-0.185	0.040	0.169
Open-field SD of speed	0.832*	-0.329	0.114	0.029	0.046
Voluntary 5.5 m speed	0.690*	0.286	0.127	0.172	0.341
Forced sprint speed	0.583*	0.359	-0.397	-0.351	-0.037
Swimming endurance	-0.056	-0.089	0.749*	-0.466*	0.315
Wheel running, day 1	0.077	0.518*	0.423	0.353	-0.580*
Wheel running, day 7	0.328	0.699*	0.335	0.203	0.163
$\dot{V}_{O_2\max}$ residual	0.522*	0.541*	-0.204	-0.293	-0.071
Eigenvalue	3.638	1.832	1.246	1.131	0.869
% of variance explained	33.1	16.7	11.3	10.3	7.9
Cumulative % explained	33.1	49.7	61.1	71.3	79.2

\* Component correlations significant at approximately  $p < 0.01$ .

actively with activity in the open field (three measures of speed; Table 3, Fig. 3b). The mean speed in the open field (0.10 m/s) corresponds to a total distance traversed of about 90 m during a 15-min test. Although this may seem a considerable distance for an animal the size of a mouse, 0.1 m/s is much below the velocity at which maximal oxygen consumption is attained—approximately 0.7 m/s in these mice [unpublished data; cf. (18)]. Not surprisingly, mean speed in the open field did not correlate with  $\dot{V}_{O_2\max}$ . Maximum open-field speed ( $\bar{x} = 0.41$  m/s) was considerably higher, however, and correlated positively with  $\dot{V}_{O_2\max}$ . With the exception of  $\dot{V}_{O_2\max}$ , none of the traits we measured correlated with body mass, a finding that is generally consistent with previous studies (7,22,31,36,41).

We found no significant correlations between either mean or maximum speed in the open field and amount of wheel running on either day 1 or day 7 (Table 3). Previous studies of individual differences and/or strain comparisons in rodents are generally consistent with this finding [e.g., (8,24,35), references therein], although positive associations have sometimes been reported (13).

A priori, we expected that voluntary wheel running was the most likely behavior to show a correlation with  $\dot{V}_{O_2\max}$ . Although the two measurements were positively correlated, with the correlation becoming stronger over each of the 7 days (Fig. 4), statistical significance was never attained. Amount of daily wheel running may increase over even longer periods in rodents [e.g., (28,39)], and it might be that the correlations shown in Fig. 4 would reach statistical significance during longer test periods. Positive correlations between voluntary activity in rotation cages and basal metabolic rate have been reported previously in rats, but this is not thought to reflect any causal relationship [(21), references therein].

A somewhat surprising result was that our measure of maximum forced sprint speed over 1.0 m correlated positively with  $\dot{V}_{O_2\max}$  (Fig. 3c). Perhaps the time and exertion of our trials, involving five sprints in quick succession, each covering about six meters, was great enough that aerobic capacity had an influence on sprinting performance. Alternatively, perhaps variation in motivation or willingness to run affects both forced sprint speed and performance in the  $\dot{V}_{O_2\max}$  test in similar ways. Step-tests, such as we employed, are designed to yield physiologically limited measures of maximal oxygen consumption, but it is dif-

ficult to entirely eliminate motivational differences among individuals.

Swimming endurance capacity did not correlate with maximal oxygen consumption. This may be because the mean length of swimming (<6 min; Table 1) was too short to be greatly affected by capacities for aerobic energy production [see also (30)] [our earlier studies of younger, mixed-sex mice of this strain had yielded swimming times averaging 12.9 min ( $n = 297$ ; Garland, Hayes, and Dohm, unpublished)]. In some species of lizards,  $\dot{V}_{O_2\max}$  correlates positively with treadmill endurance when running times are relatively long [(14,16), references therein], but not in newborn snakes with average endurance times of 6 min (15), similar to the present study. It is also possible that the weights kept mice under water enough that ventilation was compromised, such that  $\dot{V}_{O_2\max}$  was not actually attained [see (30), and compare (15)]. In any case, we are unaware of any previous studies of rodents that have tested for correlations between individual differences in swimming endurance and  $\dot{V}_{O_2\max}$ ; Montoye et al. (31) report no correlation between swimming time and relative heart or liver size.

In summary, both voluntary and forced measures of running speed may correlate positively with aerobic capacity in untrained mice. In the case of voluntary wheel-running behavior, the correlation increases over time for at least 7 days, as mice tend to run greater distances over this period. Important areas for future studies will include 1) teasing apart the complementary ways in which innate individual differences in physiological capacities may influence locomotor behavior and, in turn, the extent to which differences in voluntary locomotor behavior may affect exercise capacities [e.g., (34), references in (23)] and 2) determining whether natural training in wild populations, for example during locomotor play, is common and biologically important [(16), references therein].

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