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A Multivariate Assessment of Spontaneous Locomotor Activity in the Mongolian Gerbil (*Meriones unguiculatus*): Influences of Age and Sex

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MEAD, L. A., E. L. HARGREAVES, K.-P. OSSENKOPP AND M. KAVALIERS. *A multivariate assessment of spontaneous locomotor activity in the Mongolian gerbil (Meriones unguiculatus): Influences of age and sex.* PHYSIOL BEHAV **57**(5) 893–899, 1995.—A multivariate assessment of the spontaneous locomotor activity of male and female Mongolian gerbils (*Meriones unguiculatus*) was obtained using a Digiscan automated animal activity monitoring system. Spontaneous motor activity data were collected over 1 h (5-min samples) for groups of male and female gerbils ranging from 26–341 days of age (26, 38, 62, 116, 151, 172, 196, 247, and 341). Variables examined included: total distance travelled, average distance per movement, average speed, number of horizontal movements, time in horizontal movement, time per horizontal movement, number of vertical movements, time in vertical movement, and time per vertical movement. Age had a significant effect on spontaneous activity; all measures of horizontal activity increased from preadulthood (26 and 38 days) and remained relatively constant thereafter for adults (62+ days). Vertical activity (rearing) measures were found to increase from the 62-day-old group to the 151- and 172-day-old groups and then decrease among the older groups (196+ days). Across the 12 samples, within sessions, all horizontal and vertical activity measures (except average speed) declined for both males and females. Habituation was more rapid for the preadults than for the adults on all horizontal measures except average distance per movement. No consistent sex differences in locomotor activity were found.

Gerbil *Meriones unguiculatus* Spontaneous activity Age differences Sex differences Development Digiscan

AGE-RELATED changes in locomotor activity have been documented in many rodents, including that of laboratory rats (*Rattus norvegicus*) (14,20), laboratory mice (*Mus musculus*) (21), and Mongolian gerbils (*Meriones unguiculatus*) (6,7). However, reports of age-related activity differences have not always been consistent, even within a species. Bronstein (5), for example, using female rats tested in an open field, found that juvenile rats (31 days) and adult rats (110 days) were both more active than young adult rats (70 days). In contrast, Delay (8), using male rats tested in a modified open field under various combinations of light and noise, found that, on average, 90-day-old rats were more active than either 25-day-old rats or 200-day-old rats. Other studies (14,20) have reported that the locomotor activity of male and female rats increased between preadulthood (21 or 30 days, respectively) and adulthood (62 or 90 days, respectively).

Relatively fewer studies have examined age-related changes in the activity of gerbils. Cheal and Foley (7) found that activity in gerbils increased sharply from birth to 21–28 days of age. Cheal (6) later studied the activity level of gerbils aged 6–18 months and found that it remained relatively stable. However, these results were based on the activity measure of "number of lines crossed" in 1 min in an open field. Although such a measure is appropriate for the description of general activity levels, it is inadequate for the description of the actual locomotor behavior of the animals in question, due to its simplicity and brief time period. Therefore, one of the purposes of the present study was to determine the influence of age on the spontaneous activity of the Mongolian gerbil, using a more refined method of measuring activity.

Sex differences in the activity levels of a number of rodent species have also been demonstrated. For example, female rats have repeatedly been found in the laboratory to be more active than male rats [for reviews see (2,3)]. In laboratory mice, females have also been found to ambulate more than males in open field

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tests, though this pattern is less consistently observed than in rats (2). A number of other studies have also observed that in golden hamsters (*Mesocricetus auratus*) females are more active than males (25–27). However, this pattern of greater female activity is not evident in all rodents. For example, reproductive adult female meadow voles (*Microtus pennsylvanicus*) have been found, in both the laboratory and the wild, to be less active than reproductive adult males (9,10,32).

Sex differences have also been reported in the activity patterns of Mongolian gerbils. However, the results of these studies have varied according to the method used to measure activity levels. Using running wheels, it was shown that female gerbils ran more and faster than males (21). This is in contrast to the results of a study by Cheal and Foley (7), which found no sex differences in open field locomotor activity in gerbils of varying ages. In the wild, adult male Mongolian gerbils have been reported to range more widely and exhibit higher activity levels than adult females (1).

Another aspect of spontaneous activity, which is rarely examined in studies of sex differences, is that of qualitative differences. For example, Roper (21) reported that female gerbils tested in running wheels ran more quickly and more consistently than did male gerbils. Qualitative data, however, are difficult to obtain using the measures commonly employed in the standard open field testing situation. A relatively recent method of collecting activity data, which is specifically designed to examine qualitative as well as quantitative aspects of spontaneous locomotor activity, is the Digiscan automated activity monitoring system (18,22).

The Digiscan system is an automated open field capable of assessing a large number of activity measures simultaneously. Along with providing detailed information on many aspects of behavior, the Digiscan system is also ideal for studying behavior over longer periods of time, which would not be feasible using traditional open field methods. The Digiscan apparatus has previously been used to examine the activity patterns of rats, mice, and meadow voles as well as the influences of age and sex on these patterns (15,18,28). Using this system, it has been shown that the well-known sex difference in laboratory rat activity levels does not emerge until 50–60 days of age and appears to be a result of greater movement speeds rather than a greater number of movements (11). Furthermore, use of the automated system revealed that sex differences on some measures disappear after 20 min of monitoring (12).

It was therefore considered that the Digiscan animal activity monitoring system would be ideal for studying the spontaneous locomotor activity patterns of Mongolian gerbils, along with any influences of age and/or sex on these patterns. Use of this system allowed for a more refined examination of both qualitative and quantitative aspects of locomotor behavior than previous methods had permitted.

METHOD

Subjects

Male and female Mongolian gerbils (n = 58; 26–341 days of age) obtained from nine separate litters were used. Data were collected from a minimum of six animals per litter. Gerbils were housed in same-sex litter groups (two–four per group) in clear polyethylene cages with hardwood bedding (Beta-chip). Food (Agway Prolab rodent chow, Formula 3000) and water were available ad lib, and temperature was constant at approximately 21–22°C. Animals were held under a 12-h light:12-h dark cycle with lights on from 0800 to 2000 h. Gerbils were classified as preadult or adult according to weight (1), with gerbils weighing 50 g or more at the time of testing being classified as adults. All animals 62 days of age and older fulfilled this criterion.

Apparatus

The automated activity monitoring system consisted of six Digiscan Animal Activity Monitors (Omnitech Model RXYZCM-16, Columbus, OH). Each monitor consisted of a 40 × 40-cm clear Plexiglas box with a grid of infrared beams mounted horizontally every 2.5 cm. Two tiers of beams are mounted 2 cm and 13.5 cm above the floor. The six monitors were connected to a Digiscan Analyzer (Omnitech Model DCM-8, Columbus, OH) that transmitted the activity data to a microcomputer.

During operation, the pattern of beam interruptions was recorded and analyzed by the computer for a system-differentiated multivariate assessment of activity. Nine variables, either calculated directly by the Digiscan Analyzer or derived from the measured variables, were examined:

1. Total distance (TD). The horizontal distance travelled by an animal in a given sample period.
2. Number of horizontal movements (NHM). The number of separate horizontal movements executed by an animal with a minimum stop time of 1 s to separate movements.
3. Average distance per movement (AD). Mean distance travelled per horizontal movement (TD/NHM).
4. Average speed (AS). Mean distance travelled per unit time (TD/HMT).
5. Time spent in horizontal movement (HMT). The amount of time an animal was in motion during a given sample period.
6. Time per horizontal movement (HMT/NHM). The average amount of time spent in each horizontal movement.
7. Number of vertical movements (NVM). The number of separate vertical movements (rearing) in a given sample period, separated by at least 1 s.
8. Time spent in vertical movement (VMT). The total time per sample spent in vertical movement.
9. Time per vertical movement (VMT/NVM). The average amount of time taken for each vertical movement.

Procedure

The activity of individual male and female gerbils from nine litters of various ages (26, 38, 62, 116, 151, 172, 196, 247, and 341 days of age) was recorded. Animals were tested in 10 groups of 6, usually consisting of a male and a female from each of three litters. Individual animals were tested only once and the day on which an individual animal's activity was recorded was pseudorandomly determined. Activity data were collected between 1830 and 1930 h, during the light period, for 12 consecutive 5-min sample periods. For each test session, one gerbil was placed in each of six Digiscan monitors, consisting of Plexiglas floors, walls, and a lid containing air holes. The gerbils could not see other animals being tested simultaneously. To eliminate conspecific odors, the Digiscan monitors were cleaned with a weak vinegar solution following each test session. All animals were weighed after the activity measurements had been taken.

Data Analysis

Multivariate analyses of variance (MANOVA) were used to analyze sets of the summed variables. MANOVA repeated-measures designs were used to analyze the individual variables across the 12 samples. Effects of age were initially analyzed using one-way ANOVAs, followed by post hoc tests (Least Significant Difference). Curvilinear trends were assessed for individual variables using a one-way ANOVA polynomial design. All data were analyzed using SPSS/PC+.

RESULTS

Age Effects

Horizontal Activity. All analyses of age effects were conducted on data collapsed across sex. One-way ANOVAs indicated that age had a significant effect on all horizontal activity measures (total distance travelled, average distance travelled per movement, average speed, number of horizontal movements, and time spent per horizontal movement) except for time spent in horizontal movement (Table 1). The younger (preadult) groups displayed less activity on all of the measures except time spent per horizontal movement. For this measure, all of the groups were relatively equivalent except for the 38-day-old group, which was found to spend significantly more time in each movement than the other eight groups, [$F(1, 50) = 28.000, p < 0.001$]. A typical activity pattern is shown in Fig. 1 for total distance travelled, average speed, and number of horizontal movements.

Additional ANOVAs indicated that the youngest gerbils (26 and 38 days) travelled significantly less distance overall, moved shorter distances per movement, travelled at lower speeds, and made fewer horizontal movements than adult (62+ days) gerbils (Table 2). The 26-day-old gerbils also spent less time overall in horizontal locomotion relative to adults, whereas the 38-day-old gerbils spent more time per horizontal movement than adults. Activity levels generally remained stable across the groups aged 62–341 days.

Vertical Activity. Measures of vertical activity were also examined. However, after data collection had been completed, it was determined that a number of the 26- and 38-day-old gerbils had not been tall enough to activate the second level of photobeams during rearing. Thus, analyses of age for the vertical measures excluded the two preadult groups. Despite the lack of inclusion of the youngest groups, a significant main effect of age was found for both time spent in vertical movement and for time spent per vertical movement (Table 1). Post hoc tests showed that the age effects were due to the 62-day-old group spending significantly less time overall in vertical movements ($p < 0.05$) and less time in each vertical movement ($p < 0.01$) relative to the older groups (Fig. 2).

There also appeared to be a nonlinear component to the age effects on the number of vertical movements and the time spent in vertical movements. Thus, these data were examined for nonlinear components. This analysis revealed a significant quadratic component for both measures [$F(1,37) = 6.99, p = 0.01$; $F(1, 37) = 10.37, p < 0.003$, respectively], indicating that activity rose to a peak somewhere near young adulthood (150–170 days) and then declined as the animals aged. The relationship between age and time spent in vertical movement could conceivably be

TABLE 1

ONE-WAY ANOVAs OF AGE DIFFERENCES FOR ALL RECORDED ACTIVITY VARIABLES, COLLAPSED ACROSS SEX

Measure	F-Value*	p-Value
Total distance	2.768	0.013
Average distance	3.978	0.001
Average speed	5.671	<0.001
Number of horizontal movements	3.672	0.002
Horizontal movement time	1.604	NS
Time per horizontal movement	6.426	<0.001
Number of vertical movements	1.420	NS
Vertical movement time	2.414	0.045
Time per vertical movement	6.185	<0.001

* $df = (8, 49)$ for horizontal measures and $(6, 37)$ for vertical measures.

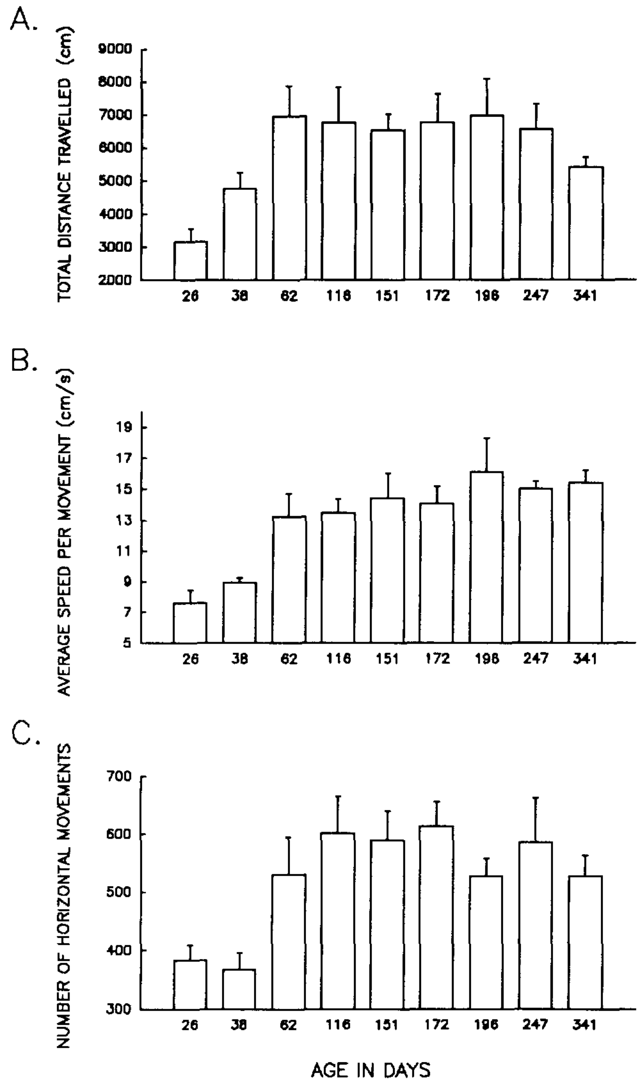

FIG. 1. The effect of age on three horizontal activity measures. These values were summed over the entire 1-h period, and are typical of the pattern shown for all nonvertical activity measures, with the exception of time spent per horizontal movement. (A) Total distance travelled. A main effect of age was found, such that activity increased from preadulthood to adulthood. Post hoc tests indicated that 26-day-old gerbils travelled significantly less distance than all gerbils aged 62 days or older, whereas 38-day-old gerbils travelled less distance than animals aged 62 and 196 days ($p < 0.05$). (B) Average speed. The main effect of age was significant, and post hoc tests indicated that 26-day-old gerbils and 38-day-old gerbils each travelled at significantly slower speeds than did any of the adult groups ($p < 0.03$). (C) Number of horizontal movements. Again, the main effect of age was significant, and each of the preadult groups made significantly fewer horizontal movements than did any of the adult groups (26 day olds, $p < 0.05$; 38 day olds, $p < 0.03$). No activity differences were found between the different ages of adult animals.

TABLE 2

ONE-WAY ANOVAs COMPARING HORIZONTAL ACTIVITY OF 26- AND 38-DAY-OLD GERBILS TO ADULT (62+ DAYS OLD) GERBILS

Measure	26 Days		38 Days	
	F-Value*	*p*-Value	*F*-Value†	*p*-Value
Total distance	15.772	<0.001	5.716	0.021
Average distance	23.857	<0.001	7.492	0.009
Average speed	23.187	<0.001	20.781	<0.001
Number of horiz. movements	11.260	0.002	17.088	<0.001
Horiz. movement time	7.324	0.009	2.312	NS
Time per horiz. movement	0.967	NS	27.997	<0.001

* $df = (1, 48)$.
† $df = (1, 50)$.

attributed to the effect of increasing age on number of vertical movements: as the gerbils aged beyond approximately 170 days, they performed fewer vertical movements, but their time in each movement stayed approximately the same, producing a lower overall time spent in vertical movements.

Duration of Activity Levels

A significant effect of time (within sessions) on activity levels was found for all horizontal and vertical measures except average speed, such that activity declined over the 12 5-min sample periods. The largest decline in activity, likely due to habituation or fatigue, occurred within the first 20–30 min, after which activity levels tended to remain constant. All of the horizontal activity measures declined more rapidly for the preadult animals (26 and 38 days old) than for the adult animals, with the exception of average distance per movement for the 26-day-old group (p-values ranged from < 0.0005 to < 0.03). Figure 3 depicts an example of this for total distance travelled. No other significant between-group differences in horizontal or vertical activity levels over time were found among the adult groups.

Sex Differences

No significant sex differences were obtained for the various activity variables. Sex differences were also absent when only the first 30 or 15 min were examined as well as when only the adult gerbils (62+ days) were included in the analyses. Although a number of significant sex by age interactions were found, no consistent pattern was obtained, either within or between measures.

DISCUSSION

The results of the present multivariate assessment of the spontaneous activity of the Mongolian gerbil revealed 1) significant age-related changes in the activity of male and female gerbils, and 2) the absence of any significant sex differences in spontaneous activity.

Age Effects

The present study examined the effects of age on activity in groups of gerbils aged 26–341 days of age, making this the most comprehensive study in this area to date. The broad range of age groups used permitted a clear description of developmental changes in the spontaneous locomotor activity of preadult and adult gerbils. Age effects were apparent on all measures. The groups aged 26 and 38 days (preadult) had lower activity scores than the adult groups (aged 62+ days) on all measures of horizontal activity, except time spent per horizontal movement. This finding is in contrast to that of Cheal and Foley (7), who reported that maximum activity levels, as measured by number of lines crossed in an open field, were reached at 21–28 days of age. This level of activity was reported to be maintained in the adults. In the present study, the youngest gerbils (26 days) displayed less activity than the adult groups on every measure of activity. The age range at which peak activity levels were reached in the present study was somewhere between 38 and 62 days, or between 5.5 and 9 weeks. Activity levels among the adult gerbils (aged 62–341 days) remained equivalent on all horizontal measures, a finding that is consistent with the Cheal studies.

The present findings are also similar to those reported for rats (14,18). Renner et al. (18), although using a much more limited range of ages (30, 60, and 90 days of age), found that 30-day-old rats had significantly lower activity levels, as measured in a modified open field, than the 60- or 90-day-old rats, but that the 60- and 90-day-old groups did not differ from each other. Similarly, Joutsiniemi et al. (14), using a continuous activity measure, found that groups of rats aged 4, 5, or 6 weeks (21–41 days old) were less active than rats aged 7–9 weeks (42–62 days) and adult rats (>62 days). In turn, rats aged 7–9 weeks were less active than the adult rats.

In the present study, vertical activity (rearing) measures were reported only for the adult groups, but even so, there was a significant quadratic component to the effect of age on two of the vertical measures (number of vertical movements and time spent in vertical movement). Vertical activity tended to increase from 62 days to 150 days, and then declined as the gerbils aged beyond 172 days. More specifically, as the gerbils' vertical activity reached a peak, the number of vertical movements increased, but the time spent in each vertical movement remained constant, resulting in a greater total amount of time spent in rearing across the 1-h sample period. In contrast, Cheal and Foley (7) reported that, in their cross-sectional study, rearing increased up to 3 months (90 days) of age and then leveled off. The Cheal follow-up study (6) reported no effect of age on rearing among 6–18-month-old (180–540 days) animals in the cross-sectional study. However, a decrease in rearing with age was reported for the longitudinally tested animals.

When habituation of activity measures was examined, it was found that all activity measures, both horizontal and vertical (with the exception of average speed), declined across the 1-h period. This activity decline occurred sooner and more rapidly in the two preadult groups, suggesting that the younger animals

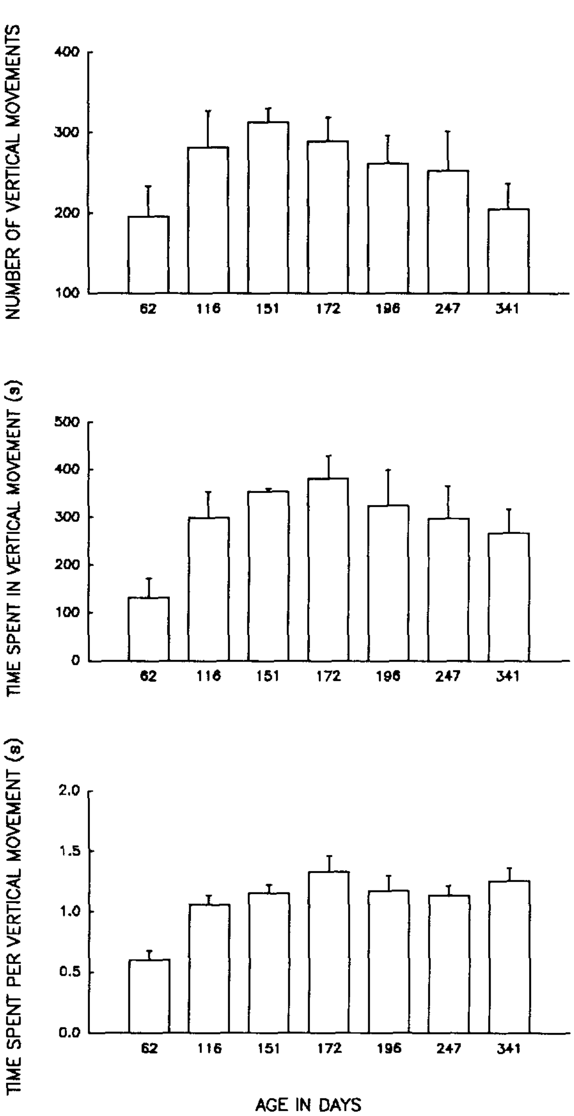

FIG. 2. The effect of age on measures of vertical activity in adult gerbils. A significant effect of age was found for the measures of time spent in vertical movement, and time spent per vertical movement, even with the exclusion of the preadult animals. For these measures, the 62-day-old gerbils engaged in less vertical activity than the older groups ($p < 0.05$). When a trend analysis was performed, it was found that the number of vertical movements and time spent in vertical movements both fit a quadratic function such that activity rose to a peak near young adulthood and then declined as the animals aged.

may have either habituated or fatigued more quickly than the older animals.

Sex Differences

No significant sex differences were found for any aspect of activity. These findings are consistent with reports by Bols and Wong (4) and Hull et al. (13) that there were no differences between male and female ambulation scores in standard open field tests. However, other gerbil studies using running wheels (21), open field tests (6,7), and direct observation in the wild (1) have reported sex differences in activity levels, with some reporting greater female activity and others greater male activity. Interpretation of these contradictory results is complicated by the variety of methods used to collect the activity data, as well as by experimental design factors such as the use of longitudinal vs. cross-sectional testing, and by characteristics of the gerbils themselves such as their age, their status as wild or laboratory-bred, and their reproductive condition.

To date, there has been only one report of a sex difference in the spontaneous activity of gerbils in the wild (1). This study reported that males ranged more widely and were more active than females. However, the data collection method for this behavior was clearly inadequate; by the authors' own admittance the activity measure they used was only a "crude measure of both the presence above ground and the tendency to be active and move about" (p. 20). Therefore, because there are, at present, no good field reports of the relative activity of male and female gerbils, laboratory activity measurements must be relied upon to estimate the natural behavior of these animals.

Two studies have found sex differences in gerbil activity measures as assessed in the traditional laboratory open field: 1) Cheal and Foley (7) reported that females reared more frequently than males when the animals were tested many times using a longitudinal design, but not when animals of varying ages were tested in a cross-sectional design; 2) Cheal (6) reported that, using a longitudinal design, adult females were more active and reared more often in the open field than did adult males. However, using a cross-sectional design, females were less active in the open field than were males. The results of these studies emphasize the influence of prior experience with a testing situation on gerbil activity levels.

It is likely that the discrepancies between the results of the present study and those of Cheal (6,7) are attributable to the differences between the activity measures used and the periods of time that the animals were monitored. The method employed by Cheal assessed the number of line crossings made by gerbils during the first minute in an open field, whereas the Digiscan apparatus allowed the assessment of many different activity measures over a 1-h period. Furthermore, it is possible that data collected during only the first minute in a novel environment is more representative of exploratory behavior than of spontaneous activity per se.

Roper's (21) report of wheel running in male and female gerbils is particularly interesting in that he observed sex differences in activity that were dependent on the phase of the circadian

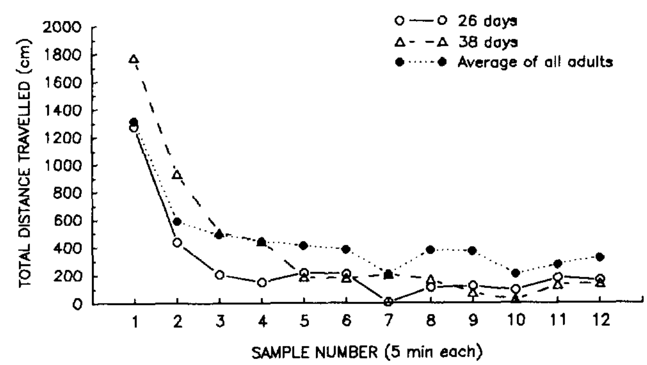

FIG. 3. Habituation effect for total distance travelled. This graph is typical of the habituation pattern shown for all nonvertical activity measures. For this measure, the activity levels of both the 26-day-old gerbils and the 38-day-old gerbils declined at a faster rate than that of the adult gerbils. No differences were found in the rate of activity decline among any of the adult groups.

light–dark cycle. Specifically, the females performed virtually 100% of their running activity during the dark phase, whereas the males, although showing an increase in activity during the dark phase, also maintained a modest level of activity throughout the light phase. As a result of these different behavior patterns, the females ran significantly more than the males during the dark phase, and the males ran significantly more than the females during the light phase. When activity levels were examined over the entire 24-h period, it was found that, overall, females ran a significantly greater number of wheel revolutions than males. These results are consistent with the notion that gerbils are primarily, though not exclusively, nocturnal (16,17,24,29).

It should be noted, however, that two studies (4,13) using a traditional open field measure (number of squares entered) failed to reveal a sex difference in nocturnal activity. In the present study, activity measures were collected during the light phase, and again, there was no evidence of a sex difference. Thus, phase of the light–dark cycle, although apparently having an effect on sex differences in wheel-running activity, appears to have much less influence on open field behaviors.

Another potentially important factor affecting the expression of sex differences in activity is reproductive status. For example, the minimum breeding age of the Mongolian gerbil is reported to be between 10 and 12 weeks (31). However, social suppression of sexual maturity, and concomitant decreases in activity levels and home range size, have been observed among wild gerbils (1). Because the gerbils used in the present experiment were housed in same-sex littermate groups, and because the animals were not examined for their reproductive status, the possibility that social suppression might have influenced the activity of some of our gerbils cannot be ruled out.

It should be noted, however, that the influence of group housing on activity levels is far from straightforward. For instance, an early study (30) reported that groups of three male gerbils housed together for 2 weeks showed decreased activity levels in an open field compared to individually housed gerbils, whereas groups of 5 or 10 male gerbils showed increased activity compared to individually housed gerbils. Thus, although it is possible that littermate housing may have influenced the reproductive condition and activity levels of some of the gerbils in this experiment, it is unlikely that this factor alone would explain the lack of sex differences in the present study.

It is also possible that direct hormonal influences played a role in our findings. The estrous cycle, for example, has been shown to have a relatively strong effect on activity levels in the female gerbil (33). However, because our animals were each tested only once and the order of testing was randomized, there is no reason to expect any systematic bias, in terms of phase of the estrous cycle.

In summary, our study has demonstrated significant effects of age on several aspects of locomotor activity in gerbils, while failing to obtain any significant effects of sex. Although earlier experiments have also directly or indirectly examined sex and age effects on activity in gerbils, use of single activity measures over very short observation times and limited age ranges have prevented definitive statements regarding the exact nature of such effects. In the present study, use of the Digiscan system allowed for the simultaneous examination of many activity variables, as well as the opportunity to determine how these measures change over time. In this way, patterns of behavior can be studied and related to one another, as opposed to providing only quantifications of gross behaviors. Multivariate studies such as these are important in that they contribute to more accurate characterizations of behavior (19), and therefore provide valuable information regarding individual and group differences.

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