Measures of Growth, Development, and Sexual Maturation in Mongolian Gerbils (*Meriones unguiculatus*): Effects of Photic Period during Ontogeny

MERTICE M. CLARK
BENNETT G. GALEF, JR.
Department of Psychology
McMaster University
Hamilton, Ontario, Canada

We examined, in Mongolian gerbils, the adequacy of two commonly used indices of rate of development, age at eye-opening and age at vaginal introitus, as predictors of biologically important events: initiation of feeding on solid food and age at first parturition. We then enquired as to the interrelationships among body weight, eye-opening, and vaginal introitus in Mongolian gerbils whose rates of development were manipulated by altering the extent of their exposure to illumination during ontogeny. We found that (1) age at vaginal introitus was significantly, but weakly, correlated with age at first parturition (Experiment I); (2) age at eye-opening strongly predicted age of initiation of gnawing on solid food (Experiment II); (3) eye-opening occurred at markedly different ages, but at the same body weight in gerbils reared under 0/24-, 6/18-, 12/12-, and 24/0-hr day–night cycles (Experiment III); and (4) vaginal introitus occurred at both different ages and different body weights in females reared under different day–night cycles (Experiment III).

In previous publications, we have described effects of exposure to illumination prior to weaning on rates of development in Mongolian gerbils (Clark & Galef, 1980, 1981). Both eye-opening and vaginal introitus occur at earlier ages in subjects maintained from birth on a 12-hr light–dark cycle than in subjects maintained in constant darkness. Although age at eye- and vaginal opening are widely used as indices of development in studies both of gerbils and other rodent species, it is not entirely clear that these convenient measures are correlated with or predictive of the occurrence of more biologically important events in the life histories of subject species (Kennedy, 1973; Kennedy & Mitra, 1963; Vandenbergh, 1967). Further, it is not known if such laboratory indices of development are correlated measures, reflecting a single underlying developmental process,

Requests for reprints should be sent to Dr. Mertice M. Clark, Department of Psychology, McMaster University, Hamilton, Ontario, L8S 4K1, Canada.

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or if each of the various indices assesses developmental processes that proceed relatively independently of one another (Tanner, 1978).

In the present paper, we first examined the relationship of age at vaginal introitus (Experiment I) and age at eye-opening (Experiment II) to two biologically important life-history events, respectively: age at first parturition and age at initiation of independent feeding. We then (Experiment III) examined the interrelationship of three commonly employed indices of developmental progress, eye-opening, vaginal introitus, and body weight, as a first step in determining whether they measure single or multiple underlying developmental processes.

Experiment I

Although it is well established that in some rodents (e.g., *Rattus norvegicus*) both first estrus and first mating occur shortly after vaginal introitus (Clark & Price, 1981), in others (e.g., *Mus musculus, Meriones unguiculatus*), pregnancy does not occur for some weeks or months following vaginal opening (Arrington, Beaty, & Kelly, 1973; Kennedy, 1973; Marston & Chang, 1965; Vandenbergh, 1967). In those species exhibiting substantial delays between vaginal introitus and first conception, age at vaginal opening could either be unrelated to the age at which individuals first reproduce or predictive of age of functional sexual maturity. If vaginal introitus were unrelated to age of first successful reproduction, it would be of questionable value, as conventionally used, as an index of rate of sexual development.

Method

Subjects

Twenty-five multiparous pairs of Mongolian gerbils (*Meriones unguiculatus*) acquired from Tumblebrook Farms (Brookfield, MA) served as the source of the 60 female pups used as experimental subjects in the present experiment. Thirty adult male gerbils, previously successfully bred in the McMaster colony, served as consorts of experimental subjects.

Breeding and Rearing Conditions

Breeding pairs were housed in 35 × 30 × 15-cm polypropylene cages lidded with 1.2-cm ($\frac{1}{2}$-in.) screen and carpeted with a thin layer of wood chips (Betta-chip, Northeastern Product Corp., Warrensburg, NY). The colony was maintained on ad lib Purina Laboratory Rodent Chow and water on a 12-hr light/dark cycle (light onset 0700 hours) throughout the study.

Breeding pairs were examined daily and when a female was visibly pregnant (third trimester), her mate was removed from her cage. Cages containing pregnant females were subsequently examined twice daily (at 1000 and 1600 hours) to determine date of parturition.

Pups were toe-clipped for individual recognition on the day of their birth (Day 1) and weaned at Day 25. During the period from birth to weaning, female pups were examined daily both for eye-opening (defined as the day on which both eyes were fully

opened) and for vaginal introitus. Examination for vaginal introitus was accomplished by applying gentle pressure immediately anterior to the vagina.

At the time of weaning, each female subject was paired with one of thirty 100–140-g males that had previously bred successfully. A male was left with his female until she was either visibly pregnant or reached 210 days of age. Each of these 30 males was paired, in counterbalanced order, with a female achieving vaginal introitus prior to Day 25 and with a female achieving vaginal introitus after Day 25.

Those females that had not exhibited vaginal introitus by the time they were weaned continued to be examined daily until vaginal introitus occurred. All females were examined weekly for evidence of pregnancy until termination of the experiment on Day 210. To control for any litter effects in the analyses reported below, no more than one female exhibiting vaginal introitus prior to Day 25 and one female exhibiting vaginal introitus after Day 25 from any single litter were retained as subjects. Early-maturing females were taken from litters averaging 6.1 (S.E. = .4) pups at birth, late-maturing females from litters averaging 6.0 (S.E. = .4) pups at birth.

Results

The main results of Experiment I are presented in Figure 1, which provides a scatter plot of the age at vaginal introitus and age at first parturition of each of the 43 of our 60 females giving birth prior to reaching 210 days of age. Examination of the figure reveals two distinct subgroups: those females exhibiting vaginal introitus on or before reaching 20 days of age ($n = 24$) and those females exhibiting vaginal introitus after reaching 25 days of age ($n = 19$). The former group of animals gave birth to their first litter at a significantly younger age ($\bar{X} = 83.2 \pm 2.3$ days) than did the latter ($\bar{X} = 111.3 \pm 7.31$ days; $t = 3.64$, $p < .01$; two-tailed t-test). For all 43 subjects, a correlation of .48 ($p < .001$) was obtained between age at vaginal introitus and age at first parturition.

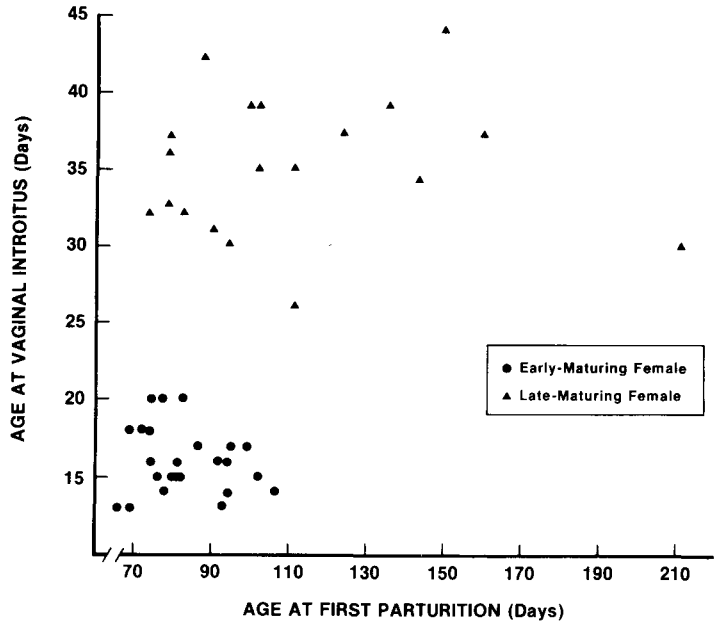

Fig. 1. Scatter diagram relating age at vaginal introitus to age at first parturition.

Six of the 30 subjects exhibiting vaginal introitus prior to reaching 20 days of age, and 11 of the 30 females exhibiting vaginal introitus after reaching 25 days of age failed to produce a litter before the end of the experiment ($X^2 = 2.06$, $p > .05$). Although seven of these 17 animals had been observed copulating, none was reproductively successful. The 71.7% reproductive success rate in the present study is within the normal fertility range for female gerbils (Arrington et al., 1973).

The observed reproductive failure of these 17 females did not appear to be a function of the age, and possible potency, of their male cohorts. Nine of the 17 females failed to breed with a male during his first pairing, eight during his second. No single male failed to impregnate at least one of the two females with which he was bred.

Discussion

The present data are ambiguous as to the usefulness of vaginal introitus as an index of sexual development in Mongolian gerbils; age at vaginal opening was significantly correlated with age at first parturition, but the former measure accounted for less than 25% of the variance in the latter.

Although age at vaginal opening does not appear to be a particularly good predictor of onset of reproduction in gerbils, as will be discussed at greater length elsewhere, the broad distinction between females exhibiting vaginal introitus at relatively early and late ages (see Fig. 1) does seem to be of considerable value. Gerbils exhibiting early vaginal introitus began reproducing earlier in life, continued reproducing to a greater age, and bore and weaned more litters, more young, and a greater percentage of female offspring than those females exhibiting late vaginal introitus (Clark & Galef, in preparation). Thus, although age at vaginal introitus is not strongly correlated with age at first reproduction, and thus age at functional sexual maturity, it is a predictor of the reproductive success a female will enjoy throughout life.

There are, of course, indices of sexual development other than age at vaginal introitus, such as age at first vaginal estrus, that might better predict age at first parturition. However, even in mature Mongolian gerbils "cellular changes in the vaginal smear are of very limited practical value in the prediction of cyclic heat and mating" (Norris & Adams, 1981; p. 193; see also Marston & Chang, 1965). We found cornified cells in all vaginal smears taken from females on the day of vaginal introitus, but the presence of these cells did not appear indicative of first behavioral estrus (unpublished observation). Further, the repeated taking of vaginal smears is an intrusive procedure that might directly affect age at first reproduction in subjects. These realities would seem to preclude the determination of a relationship in gerbils between first vaginal estrus and first parturition that would differ in a meaningful way from that observed between vaginal introitus and first parturition.

Experiment II

Like other rodent species, Mongolian gerbils initiate feeding on solid food at about the time at which eye-opening occurs (DeGhett, 1972; Galef, 1979; Kaplan & Hyland, 1972; McManus, 1971). Because eye-opening in a population of young gerbils occurs over a period of days (from Days 17–21 postpartum; Clark & Galef, 1981), it is possible to examine the relationship between eye-opening and initiation of feeding by examining

the onset of weaning in subjects whose eyes open at different chronological ages. In Experiment II, the weaning of pups whose eyes opened by Day 18 was compared with that of pups whose eyes opened after Day 18.

Method

Subjects

Thirty-six male Mongolian gerbils, selected from 31 litters born and reared in the McMaster colony, served as subjects. We used as subjects only those pups both of whose eyes were fully open on Day 18 ($n = 19$) or still sealed on Day 18 [i.e., both of whose eyes were open on Day 19 ($n = 14$), Day 20 ($n = 2$), or Day 21 ($n = 1$)]. Because pups were examined for eye-opening twice/day and because eye-opening is a continuous process, pups, one of whose eyes were open at the time of inspection on Day 18, might have, in fact, opened both eyes later on Day 18. Selection of subjects as described above removed much of the ambiguity in assigning an age for eye-opening to pups.

Breeding and Rearing Conditions

Housing and maintenance of breeding pairs was as described in Experiment I. Subjects were weighed daily from Day 1 (day of birth) to Day 25 (weaning) and, starting on Day 15, were examined twice daily for eye-opening.

Each subject was observed for 1 hr/day from Day 13 to Day 25 in the apparatus described below.

Weaning Test Procedure

Each subject was removed from its home cage between 1100 and 1200 (during the light phase of the day–night cycle) and individually transferred to a Plexiglas chamber [7.5 × 7.5 × 7.5 cm, with a 1.22-cm ($\frac{1}{2}$-in.) screen lid] maintained in a temperature-controlled water bath (33°C). Each chamber contained three pellets of Purina Laboratory Rodent Chow, three hulled sunflower seeds, and six wood chips. An observer recorded whether each subject mouthed food and nonfood items during each daily 1-hr test period. Chambers were cleaned and both food and nonfood items replaced after testing of each subject.

Results

Figure 2 shows the percentage of pups whose eyes opened either by Day 18 or after Day 18 that gnawed on food (left-hand panel) or nonfood items (right-hand panel) during daily 1-hr tests. As can be seen in Figure 2, subjects whose eyes opened by Day 18 began gnawing on solid objects at an earlier age than did those whose eyes opened after Day 18 (Fisher exact probability test: $p < .01$; two-tailed). A delay of approximately 1 day in eye-opening resulted in a 1-day delay in onset of gnawing. Although a single day's delay in the onset of weaning-related activity may seem trivial, it had observable consequences for the growth rate of pups. Body weight of those pups whose eyes opened

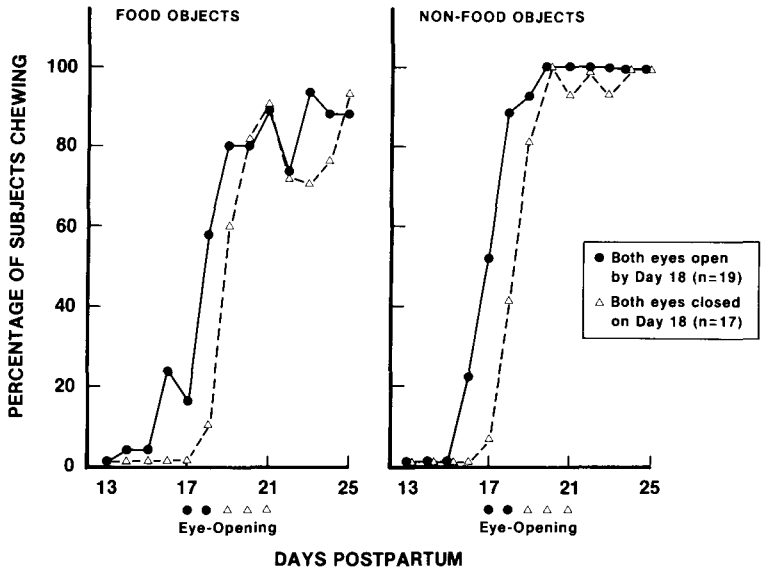

Fig. 2. Percentage of gerbil pups observed gnawing on food and nonfood objects as a function of age at eye-opening.

by Day 18 increased 39.6% between Days 18 and 25 (the age at which we removed them from their dams), while those whose eyes opened after Day 18 grew by only 28.7% during the same period (two-tailed t-test: $t = 1.99$, $p < .05$).

Pups exhibiting eye-opening prior to Day 18 weighed the same amount at birth as those exhibiting eye-opening after Day 18 (3.0 ± .3 g for both groups) and both groups of pups exhibited equal rates of growth during the week preceding eye-opening (respectively, 56.2 and 54.4% increases in body weight; $t = .028$, $p =$ n.s.). The fact that gnawing (and presumably ingestion) of solid foods attends eye-opening provides a plausible explanation of the enhanced growth observed in pups exhibiting eye-opening at a relatively early age, and our test procedure thus seems to provide a reasonable index of age at weaning.

Age at eye-opening was not predictive of age at first parturition in females; those females exhibiting eye-opening by Day 18 gave birth to first litters at a slightly, but not significantly, earlier age (91.7 ± 7.4 days) than those exhibiting eye-opening after Day 18 (98.0 ± 5.5 days; $t = .69$, $p =$ n.s.).

Discussion

The results of Experiment II indicate that age at eye-opening is a good predictor of age of initiation of gnawing and of future rates of growth. It thus appears to correlate highly with the onset of weaning. Age at eye-opening fails to predict age at first parturition in females.

Experiment III

Several conventional measures of rate of development of Mongolian gerbils are affected by the duration of the light portion of the day–night cycle in which developing young are maintained. Gerbils reared on a 12-hr light/dark cycle exhibit both eye-opening

and vaginal introitus at an earlier age than those reared in constant dark and pups reared on a 12-hr dark/light cycle grow considerably more rapidly than those reared in the dark (Clark & Galef, 1980, 1981).

It has been suggested that ontogenetic landmarks, such as eye-opening and vaginal introitus, occur when animals achieve a critical body weight and/or body composition (Engle, Crafts, & Zeitham, 1937; Frisch, 1972; Frisch & Revelle, 1970). In this view, delays in sensory development and sexual maturation observed in gerbils reared in the dark (Clark & Galef, 1981) would be a consequence of their reduced rate of increase in body size. Alternatively, body weight *per se* may not be a determinant of other measures of development (Ramalay, 1979; Wilen & Naftolis, 1977; Vandenbergh, Drickamer, & Colby, 1972); exposure to relatively short periods of illumination during ontogeny might inhibit sensory and sexual maturation independently of its effects on body weight.

In the present experiment, litters of gerbils were reared under four different dark/light cycles and the age and body weight at which eye-opening and vaginal introitus occurred was compared across rearing conditions.

Method

Subjects

Subjects were 80 litters of Mongolian gerbils born in the McMaster colony to multiparous breeding pairs acquired from Tumblebrook Farm (Brookfield, MA). Maintenance conditions in the colony were as described in Experiment I.

On the day of parturition (Day 1), each litter was culled to two male and two female pups. Those litters with fewer than four pups were not used in the experiment and any litter containing four or more pups on Day 1, but two or fewer on Day 25, was similarly discarded and replaced, until 20 litters had been successfully reared in each of the four photic conditions described below.

Procedure

Rearing conditions. On Day 1, litters and their parents were randomly assigned to one of four photic conditions and moved to experimental rooms maintained either in constant light (Group 24-hr L), on a 12-hr light/dark cycle (Group 12-hr L), on a 6:18-hr light/dark cycle (Group 6-hr L), or in constant darkness (Group 0-hr L). Illumination, when needed, was provided by two 35-W Westinghouse Cool-White fluorescent bulbs located approximately 2 m above the tops of the cages (35 × 30 × 15 cm) in which litters were maintained.

Each litter was left in its respective photic environment with ad lib access to Purina Laboratory Rodent Chow and water until Day 45. Litters were disturbed (1) when their parents were removed on Day 30; (2) when cages were cleaned on Days 15 and 30; and (3) for the experimental procedures described below.

Experimental procedure. Each pup was weighed on Day 15 and every 5 days thereafter until Day 45. Beginning on Day 15, each subject was examined daily, males for eye-opening and females for both eye-opening and vaginal introitus. On the day of eye-opening (defined as the first day on which both eyes were fully open) and the day of vaginal introitus, body weights were recorded. Subjects in Group 0-hr L were weighed and examined under dim red light; those in other groups during the light portion of the cycle.

Statistical analyses. To control for litter effects, litter means rather than data from individual subjects were used as data points in analyses of rates of growth.

Results

Growth Rate

As can be seen in Figure 3, and as we have reported previously (Clark & Galef, 1981), manipulation of the duration of light exposure during ontogeny altered the rate of growth of both male and female gerbil pups. Photic condition during rearing had significant effects on the rate of growth of both male and female pups as measured by body weight on Day 45 (males: $F = 5.22$, $df = 3,79$, $p < .01$; females: $F = 2.81$, $df = 3,76$, $p < .05$). *Post hoc* comparisons revealed that, at Day 45, both males and females reared either in constant light or on a 12/12-hr light–dark cycle weighed significantly more than those reared in constant dark or with exposure to light for 6 hr/day (Newman-Keuls tests; all p's $< .05$). No other differences were significant (Newman-Keuls tests; all p's $> .05$).

Eye-Opening and Eye-Opening × Body Weight

Figure 4 shows both the age at eye-opening and body weight on the day of eye-opening of male and female subjects in Experiment III. Both male and female subjects exhibited significant variation in age at eye-opening as a function of duration of light exposure during ontogeny ($F = 3.84$, $df = 3,296$, $p < .05$), but for both males and females, eye-opening occurred at a relatively constant weight ($F = 1.63$, $df = 3,272$, $p > .05$).

Sex of subject had no significant effect on either age ($F = .43$, $df = 1.296$, $p > .05$) or body weight ($F = .43$, $df = 1/272$, $p > .05$) at eye-opening.

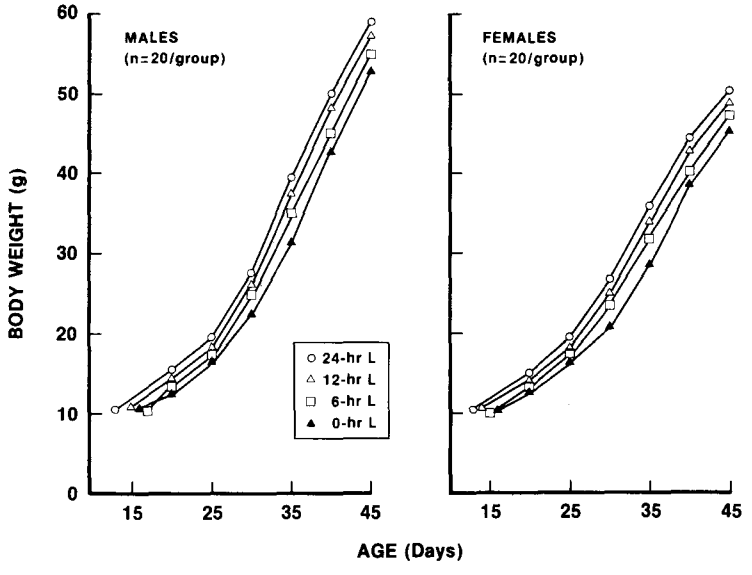

Fig. 3. Growth of male and female gerbil pups raised in four photic conditions.

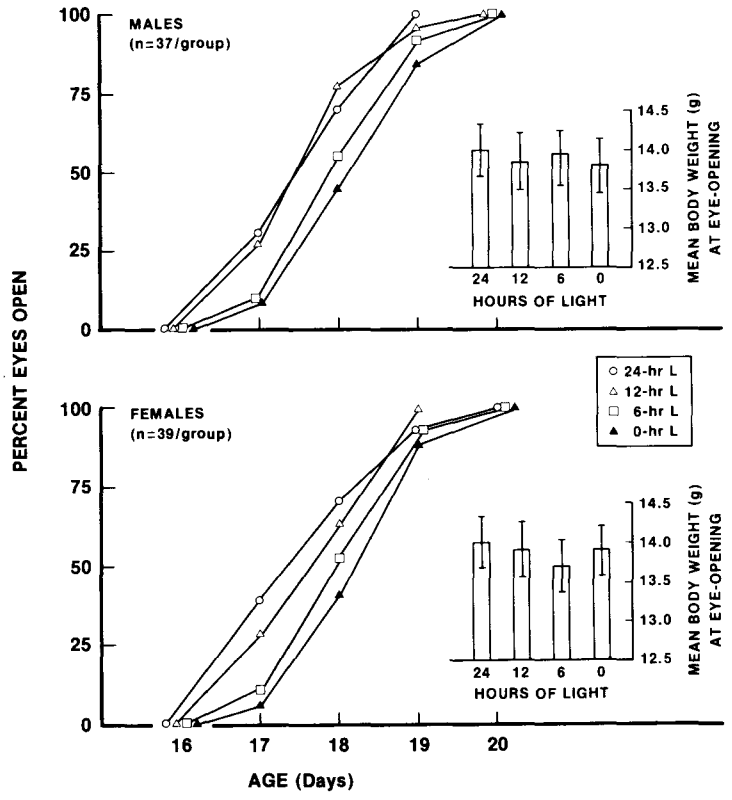

Fig. 4. Age and mean body weight at eye-opening of male and female subjects reared under four photic conditions. Flags = ±1 SE.

Vaginal Opening and Vaginal Opening × Body Weight

Figure 5 shows the cumulative distribution of age at vaginal introitus of females reared in each of the four photic conditions. As examination of Figure 5 suggests and statistical tests confirmed, there were significant differences among groups in age at vaginal opening ($F = 6.24$, $df = 3,152$, $p < .01$). Exposure during ontogeny to either constant light or a 12/12 light–dark cycle resulted in vaginal opening at an earlier age than either rearing in constant dark or in 6 hr of light/day (Newman-Keuls tests; all p's $< .05$). No other differences were significant (Newman-Keuls tests; all p's $> .05$).

Figure 5 also shows the mean and standard error of female body weights on the day of vaginal opening. Once again, there was significant variation across groups as a function of rearing condition ($F = 2.76$, $df = 3,152$, $p < .05$).

In a *post hoc* analysis, we examined the body weights of females at vaginal opening as a function of the age of occurrence. Figure 6 shows the weight of females in each of the four photic conditions on the day of vaginal introitus as a function of the age at which vaginal introitus occurred. As can be seen in Figure 6, and as statistical tests confirmed, there was no significant variation in the body weights of females reared in the four photic conditions who exhibited vaginal introitus at a particular age ($F = 1.00$, $df = 3,135$, $p > .05$). There was, however, a significant monotonic increase in the weight of females at vaginal introitus with increasing age ($F = 12.53$, $df = 3,135$, $p < .01$).

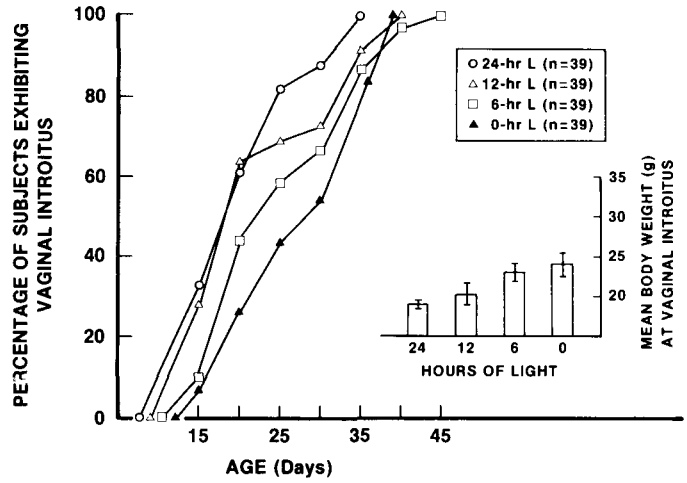

Fig. 5. Age and mean body weight at vaginal introitus of female gerbil pups reared under four photic conditions. Flags = ±1 SE.

Eye-Opening × Vaginal Introitus

A Spearman correlation coefficient between age at eye-opening and age at vaginal introitus across all 156 females (39 in each of four photic conditions) yielded a *rho* of .22 ($t = 2.80$, $p < .01$). Although the correlation was significant, variance in age at eye-opening accounted for less than 5% of the variance in age at vaginal introitus. This relative independence of age at eye-opening and age at vaginal introitus is not consistent with the hypothesis that age at eye-opening is an index of general rate of maturation.

Discussion

The results of Experiment III are consistent with the hypothesis that body weight is a determinant of eye-opening in Mongolian gerbils. Subjects differing widely in the rate of growth all exhibited eye-opening upon reaching similar body weights.

Age at vaginal introitus in female Mongolian gerbils was not related to body weight in nearly so straightforward a fashion. Females in the various photic conditions exhibited vaginal opening at significantly different body weights. However, the findings that females exhibiting vaginal opening at similar ages did so at similar body weights, regardless of photic condition during rearing, suggests that body weight does play a role in triggering vaginal introitus. Body weight appears to interact with chronological age, so that the body weight necessary for vaginal opening increases with increasing age.

General Discussion

The results of the present series of experiments suggest the following about Mongolian gerbils: (1) Age at vaginal introitus is a marginally useful index of development of reproductive competence, significantly, but weakly, correlated with first successful breeding. (2) Eye-opening is a predictor of initiation of independent feeding. (3) The two developmental measures (age at eye-opening and age at vaginal introitus) are nearly independent, with age at eye-opening being closely tied to body weight and age at vaginal introitus, only weakly so.

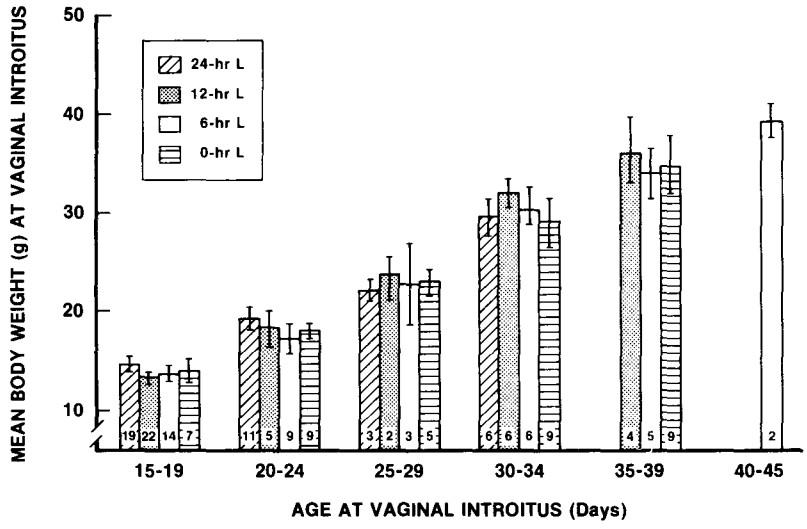

Fig. 6. Mean body weight on the day of vaginal introitus of female gerbils achieving vaginal introitus at different ages. Flags = ±1 SE.

Our data are relevant to a large, diffuse, and relatively contradictory literature concerning the relationship between body weight and onset of sexual maturity in rodents. In *Mus musculus*, the two variables have been found to be both uncorrelated (Drickamer, 1974, 1975, 1981; Hansen, Schillo, Hinshelwood, & Hanser, 1983; Vandenbergh, 1967; Vandenbergh et al., 1972) and correlated (Drickamer, 1976; Kennedy & Mitra, 1963; Montiero & Falconer, 1966). Similarly, in rats, body weight and vaginal opening have sometimes been found to be correlated and sometimes not [see Mandl & Zuckerman (1952) for a review of the data]. In the studies most similar to the present one, Hansen et al. (1983) found age at vaginal opening in mice to be independent of photoperiod, but these investigators introduced the photoperiod manipulation only a few days before vaginal introitus occurred. Drickamer (1975) found that mice raised in different photoperiods matured sexually (as measured by first oestrus) at the same mean body weight, but at different ages. His results differ from those of Experiment III, above, in which age at vaginal opening was found to be relatively independent of body weight. Whether the different outcomes of our study and that of Drickamer reflect differences in species or dependent variable examined is not clear. In either case, our data are more consistent with those reports failing to find a close link between body weight and sexual maturity than with those reports emphasizing such a link.

It was not our intention to become enmeshed in the controversy over the role of body weight in triggering sexual maturity. Rather, we were attempting to establish the usefulness of various indices of development in Mongolian gerbils and their degree of relatedness. Our results suggest that (1) both body weight and eye-opening are useful predictors of the onset of weaning, (2) in gerbils, unlike rats, vaginal introitus is not closely related to more direct measures of fecundity, and (3) the two measures, eye-opening and vaginal introitus, are not meaningfully related to each other.

Notes

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