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Postnatal Effects on Reproduction and Maternal Care in Early- and Late-Maturing Gerbils

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CLARK, M. M. AND B. G. GALEF, JR. *Postnatal effects on reproduction and maternal care in early- and late-maturing gerbils*. PHYSIOL BEHAV **36**(6) 997–1003, 1986.—In previous papers, we have identified a number of differences in both the reproductive profiles and patterns of maternal care shown by female gerbils exhibiting vaginal opening either before or after weaning. Early-maturing females delivered their first litters when younger, produced a greater percentage of female offspring/litter, and a greater percentage of early-maturing daughters than late-maturing females. Further, early-maturing females exhibited reduced levels of maternal care, as assessed by time spent nursing, time pups were gathered in the nest, and probability of retrieval of displaced young. In the present experiments, we found that equating age at first parity of early- and late-maturing females (Experiment 1) eliminated differences between them in pup gathering, but not in pup retrieval or nursing. Further, equating age at first parity affected neither sex-ratios of litters at birth nor rate of maturation of daughters. Equating litter size at birth, sex-ratio of litters at birth, and maternal age at first parturition (Experiment 2) eliminated differences in the nursing behavior of early- and late-maturing females and reduced differences in retrieval behavior, but left rate of maturation of daughters unaffected. Last (Experiment 3), both daughters born to early-maturing females, reared by late-maturing females, and daughters born to late-maturing females, reared by early-maturing females, exhibited rates of maturation typical of daughters reared by their natural mothers.

Maternal age Litter size Fostering Sex ratio Puberty

RESULTS of recent studies in our laboratory [2,3] have shown that age at vaginal opening is bimodally distributed in the strain of domesticated Mongolian gerbil (*Meriones unguiculatus*) currently available in North America. Within a randomly-mated colony of domesticated gerbils maintained in a single colony room, we found both precocious females, exhibiting vaginal opening prior to reaching 23 days of age (mean=15.9±0.5 days), and late-developing females that failed to exhibit vaginal opening until they were more than 27 days of age (mean=35.2±0.7 days) [2,3]. Review of the field literature indicates that accelerated puberty, as measured by weight at first pregnancy, occurs in free-living wild gerbils [16] as well as in domesticated gerbils (see [3] for discussion).

In domesticated gerbils, unlike domesticated mice [8,9], age at vaginal opening is a predictor of subsequent reproductive and maternal behaviors [2,3]. We have found a highly significant positive correlation between age at vaginal opening and age at first parturition in laboratory-reared gerbils [2]. Further, early-maturing female gerbils first reproduced when younger, produced more litters during their lifetimes, slightly (but not significantly) more young/litter, and, consequently, more than twice as many offspring as late-maturing females. Early-maturing females also both gave birth to and weaned a greater proportion of females/litter and a higher proportion of early-maturing daughters/litter than late-maturing females [3]. Further, early- and late-maturing female gerbils differed in their maternal behaviors. Early-maturing females spent less time nursing their young, were less likely to have their young gathered in the nest, and retrieved fewer young displaced from the nest than late-maturing females [3].

Although our previous studies have established the existence of differences in both reproductive and maternal behaviors of early- and late-maturing female gerbils, they provide no information on the causes of these differences. In the present paper, we begin analysis of the factors responsible for observed differences in the reproductive profiles and maternal behaviors of early- and late-maturing female gerbils by examining the possibility that any of a variety of postnatal factors might be causally related to observed differences in their behavior.

First, as mentioned above, early-maturing female gerbils gave birth to their first and subsequent litters at an earlier mean age than did late-maturing females. It is possible that maternal behavior in gerbils varies as a function of age. Differences in maternal behavior of mothers of different ages might affect development of their daughters (for an analogous case in male rats see [15]) resulting, for example, in daughters born to younger females developing more rapidly

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than daughters born to older females. Older female gerbils might also deliver smaller or more male-biased litters than young ones [1, 5, 6, 12, 19, 20]. Thus, variance in the age of mothers at first parturition might be responsible for observed differences in their maternal behavior and development of their respective young.

Second, early-maturing females matured in larger litters than late-maturing females. Studies of both gerbils and other rodent species suggest that relatively small litters receive different patterns of maternal care than relatively large ones [10, 11, 17, 21, 26]. Again, such differences in patterns of maternal care might affect subsequent rate of development of daughters and their offspring.

Last, late-maturing mothers reared daughters in predominantly male litters, while early-maturing females raised daughters in predominantly female ones. Drickamer [7] has shown in mice that presence of males in a litter retards rate of development of female littermates. It is possible that the concordance in rate of maturation of mothers and daughters mentioned above results from similarities in the sex-ratios of the litters they produce.

In the experiments described below, we determined effects of maternal age on maternal behavior, sex-ratios of litters, and rate of development of daughters. We also examined effects of litter size and natal sex-ratio of litters on maternal behavior and rate of sexual development of female litter members.

GENERAL METHOD

Multiparous breeding pairs of Mongolian gerbils acquired from Tumblebrook Farm (Brookfield, MA) served as the source of all subjects. Breeding pairs were housed in polypropylene cages (35×30×15 cm) with hardware-cloth (1.27 cm) lids. Each cage was carpeted with a thin layer of woodchip bedding (Betta-chip, Northeastern Products Corp., Warrensburg, NY). The colony was maintained on ad lib Purina Laboratory Chow and water in a single, temperature-controlled colony room illuminated on a 12-hr light-dark cycle (lights on at 700 hours). Breeding pairs were examined daily and, when the female was visibly pregnant (last third of pregnancy), her mate was removed from her cage. Cages containing pregnant females were examined twice daily (1000 and 1500 hr) to determine date of parturition.

Pups in each litter were toe-clipped for individual recognition on the day of their birth (Day 1) and weaned to a cage separate from their dam on Day 25. During the period from birth to weaning, all female young were examined daily to determine age at vaginal opening. Examination for vaginal opening was accomplished by applying gentle pressure just below the vagina. Those females that had not exhibited vaginal opening before weaning continued to be examined daily until vaginal opening had occurred.

Females exhibiting vaginal opening before Day 25 were classified as early-maturing and those achieving vaginal opening after weaning, as late-maturing. As we have shown previously [3], age at vaginal opening is bimodally distributed in domesticated gerbils. Thee was no overlap in the ages at which early-maturing females (mean=16.5±0.7 days) and late-maturing females (mean=37.1±0.8 days) exhibit vaginal opening in the present experiments. Because we weaned our gerbils at 25 days of age, it was convenient to use a criterion of vaginal patency at Day 25 to discriminate early- from late-maturing females, but any criterion from Day 23 to Day 27 would have served equally well as none of our subjects exhibited vaginal opening during that period.

Except where indicated, all p values reported below are for 2-tailed tests.

EXPERIMENT 1

If differences in reproductive profiles and maternal behaviors of early- and late-maturing females reflect differences in their respective ages at first parturition, one would expect early- and late-maturing females reproducing for the first time at the same age to produce litters of similar size and sex-ratio, and to have daughters that matured at the same rate. Further, one would expect such females to exhibit similar patterns of maternal behavior. In the present experiment, we compared reproductive profiles and maternal behaviors of: (1) early-maturing females placed at weaning with sexually mature males (Early-maturing, early-bred Group), (2) early-maturing females placed with sexually mature males at 90–110 days of age (Early-maturing, late-bred Group), and (3) late-maturing females placed with sexually mature males at 90–110 days of age (Late-maturing, late-bred Group).

METHOD

Subjects

Forty-four females from 27 litters reared in the McMaster colony, as described in the General Method section, served as subjects. At weaning, each subject was assigned to one of three treatments; 10 subjects to the Early-maturing, early-bred Group, 17 to the Early-maturing, late-bred Group and 17 to the Late-maturing, late-bred Group. All 10 females in the first group, 15 of those in the second and 14 of those in the third produced a litter before reaching 210 days of age. All 10 females in the first group, 14 of those in the second, and 12 of those in the third reared some pups to weaning.

Procedure

Breeding. Each subject in the Early-maturing, early-bred Group was paired with an adult male of proven fertility on the day of weaning (Day 25). Subjects in Early-maturing, late-bred and Late-maturing, late-bred Groups were placed in sibling pairs until they were 90–110 days of age, at which time each was placed with a proven adult male. Each subject was left with her mate until she was either visibly pregnant or reached 210 days of age, whichever occurred first.

Pups born to subject females were counted, sexed, and toe-clipped for individual recognition on their day of birth (Day 1). Pups were counted for a second time at weaning (Day 25). Each female pup born to subjects in the three groups was examined daily from birth to weaning to determine her age at vaginal opening.

Testing. Maternal behavior of subjects was examined using three indices: a measure of nursing, a measure of gathering, and a measure of retrieval. Nursing and gathering were assessed by examining the cage of each subject twice daily (1000 and 1500 hr) from parturition to weaning to determine whether, at the time of inspection: (1) all pups were gathered in the nest and (2) the dam was in a nursing posture over the pups and the pups were attached to the dam's nipples. Each dam was awarded two scores from 0–10 (2 inspections/day × 5 days) indicating the number of inspection periods in a 5-day block during which (1) her pups were gathered in the nest and (2) the dam was nursing her young. For purposes of statistical analysis, each female was as-

TABLE 1

CHARACTERISTICS OF FIRST LITTERS DELIVERED AND WEANED BY SUBJECTS IN EXPERIMENT 1

Maturation: Breeding: N:	Early Early 10	Early Late 15	Late Late 14
Mean age at first parturition*	83.1 ± 6.6†	138.0 ± 4.3	147.0 ± 6.3
Mean litter size at			
Birth	7.2 ± 0.7	7.0 ± 0.4	6.4 ± 0.6
Weaning	5.6 ± 0.5	4.7 ± 0.5	4.2 ± 0.8
Mean percent males/litter at			
Birth*	43.6 ± 3.7	47.8 ± 5.0	61.6 ± 5.6†
Weaning*	40.6 ± 6.7	49.7 ± 5.6	69.7 ± 6.4†
Mean percent early-maturing daughters/litter*	58.4 ± 11.4	62.6 ± 10.8	34.8 ± 7.6†

*F ratios significant ($p<0.05$).
†Group differs ($p<0.05$) from the other two groups in its row.
Measures of variance are S.E.M.s.

signed a single nursing and a single gathering score based on all 50 (2 inspections/day × 25 days) observations of that female.

Retrieval of subjects was assessed on Day 10 postpartum when each dam was tested for her response to displacement of two of her own pups from the nest. The experimenter picked up the dam from the nest, removed two pups (1 male and 1 female, when possible), lowered the dam back on the nest, and placed the two pups in the corner of the home cage diagonally opposite the nest. During the 5-min period following pup displacement, the experimenter observed behavior of the dam. Retrieval testing was conducted blind.

Statistical Analysis

One-way ANOVA was used to compute effects of maternal age at parity on reproductive and maternal behaviors. Protected t-tests appropriate for unequal Ns [6] were used in all *post hoc* analyses.

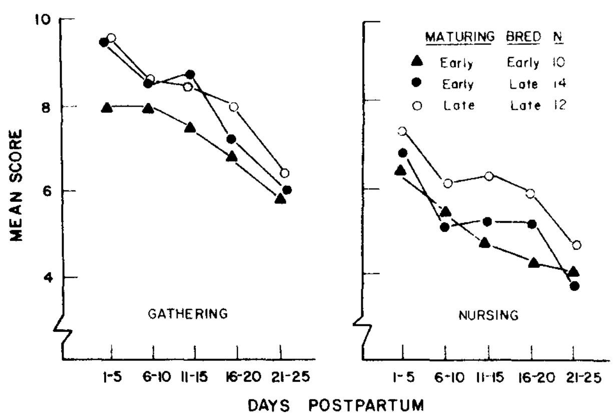

FIG. 1. Mean gathering (left-hand panel) and nursing (right-hand panel) scores of females in the three groups of Experiment 1.

RESULTS

The main results of Experiment 1 are shown in Table 1 and Figs. 1 and 2. As can be seen in Table 1, litters born to early-maturing early-bred females (mean age at vaginal opening 17.1±0.7 days) differed in a number of ways from those born to late-maturing, late-bred females (mean age at vaginal opening 37.0±1.6 days). Litters of early-maturing, early-bred subjects were slightly, but not significantly larger (both ts<1.59, both ps>0.10), contained a smaller proportion of males at both birth and weaning (both ts>2.45, both ps<0.05) and a greater percentage of early-maturing daughters, $t=2.06$, $p<0.05$, than those of late-maturing subjects. Reproductive profiles of early-maturing subjects bred late (mean age at vaginal opening 16.4±0.8 days) closely resembled those of early-maturing females bred early in spite of the fact that members of the former group gave birth both at approximately the same mean age as late-maturing subjects bred late and at a significantly greater age than early-maturing females bred early, $t=6.69$, $p<0.01$. Age at first parturition was not a determinant of the differences in sex composition normally seen at birth in early-maturing and late-maturing female gerbils, nor did it affect rate of maturation of daughters.

There is some suggestion in the data presented in Table 1 that the greater mortality rate of pups from birth to weaning seen in litters born to late-bred females may be age-related, but differences in mortality rate of pups in the three groups were not statistically significant (Kruskal-Wallace one-way ANOVA, H=2.84, $p>0.05$). Although the rate of loss of pups in the three groups (21.7, 28.1, and 32.7 percent) may seem high to those unfamiliar with reproduction in gerbils, it is well within the normal range (approximately 30 percent [14]).

Figures 1a and 1b present, respectively, data describing gathering and nursing behaviors of females in the three groups. There was a main effect of groups on both nursing, $F(2,33)=4.20$, $p<0.05$, and gathering, $F(2,33)=7.26$, $p<0.01$, behaviors. *Post hoc* tests [6] revealed that, compared with early-maturing, early-bred females, late-maturing, late-bred females were more likely to be observed nursing their young,

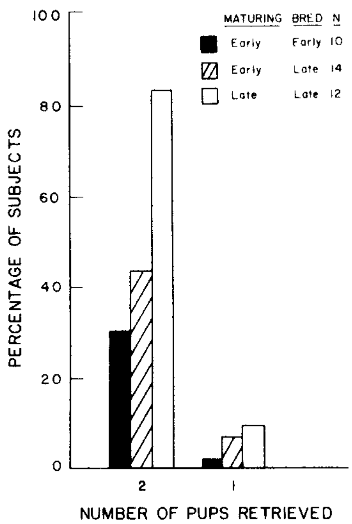

FIG. 2. Percentage of females in the three groups of Experiment 1 retrieving one or both of their pups when tested on Day 10 postpartum.

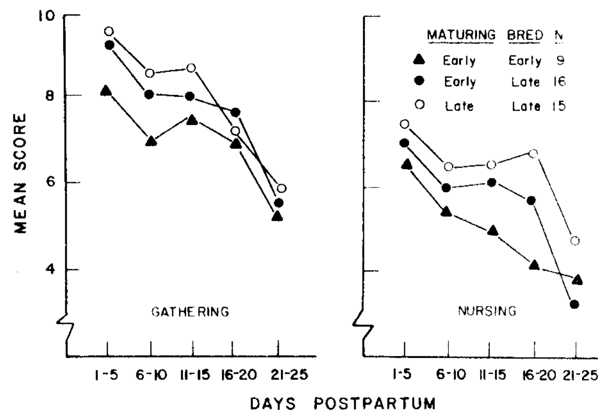

FIG. 3. Mean gathering (left-hand panel) and nursing (right-hand panel) scores of females in the three groups in Experiment 2.

$t=3.33, p<0.01$, and their young were more likely to be found in the nest, $t=4.40$, $p<0.01$. Further, nursing scores of early-maturing, late-bred females were significantly lower than those of late-maturing females bred late, $t=2.15$, $p<0.05$, while gathering scores of early-maturing females bred late were significantly greater than those of early-maturing females bred early, $t=3.50$, $p<0.01$. Thus, age at parturition affected gathering but not nursing behavior.

Figure 2 shows the percentage of subjects in each group retrieving one or both pups during the retrieval test on Day 10 postpartum. Late-maturing females bred late retrieved their young more frequently than early-maturing females bred early (Fisher's Exact Test, $p<0.01$, one-tailed test). Early-maturing females bred late retrieved their pups significantly less frequently than late-maturing females bred late (Fisher's Exact Test, $p=0.05$, one-tailed test) and with the same frequency as early-maturing females bred early (Fisher's Exact Test, $p>0.05$, one-tailed test). Age at parturition did not affect retrieval behavior.

DISCUSSION

Taken together, the results of Experiment 1 suggest that age of a female at parturition is not an important determinant of differences in reproductive and maternal behavior seen in early- and late-maturing gerbils. Equating age at first parity of early- and late-maturing females did not cause early-maturing females to produce smaller litters or litters with the sex-ratio or percentage of early-maturing daughters typical of late-maturing females. Similarly, delaying first parity in early-maturing females did not significantly affect their nursing or retrieval behaviors, though it did affect their gathering behavior. In general, it appears that differences in reproductive and maternal behaviors exhibited by early- and late-maturing gerbils cannot be explained in terms of differences in their ages at first parity.

EXPERIMENT 2

As mentioned in the introduction, early-maturing gerbil females produce relatively large, female-biased litters. Late-maturing females produced relatively small, male-biased litters. Differences in sexual composition of litters in which daughters of early- and late-maturing females developed might influence their rate of sexual maturation. Differences in size or sex-ratio of litters born to early- and late-maturing females might affect their dams maternal beahvior. Further, differences in sex-ratio of litters or differences in litter size might interact with differences in maternal age to influence both maturation of daughters and maternal behavior of mothers. In the present experiment, we held constant both the size and sex-ratio of litters born to early- and late-maturing females (the former bred both early and late) and examined the effects of these manipulations on rate of sexual maturation of female young and maternal behavior of their mothers.

METHOD

Subjects

Forty-four females from 27 litters reared in the McMaster colony, as described in the General Method section, served as subjects. At weaning, each subject was assigned to one of three Groups: 10 to the Early-maturing, early-bred Group and 17 to each of the Early-maturing, late-bred and Late-maturing, late-bred Groups. Nine subjects in the first group, 16 in the second, and 15 in the third gave birth prior to reaching 210 days of age. Each of these 40 females reared some of their pups to weaning.

Procedure

The procedure was identical to that of Experiment 1 except that litters born to subject females were culled to 2 male and 2 female pups on their day of birth.

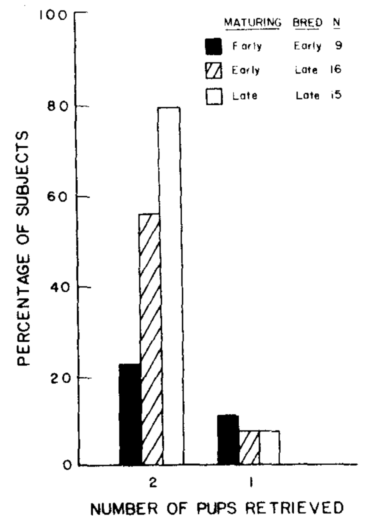

FIG. 4. Percentage of females in the three groups of Experiment 2 retrieving one or both of their pups when tested on Day 10 postpartum.

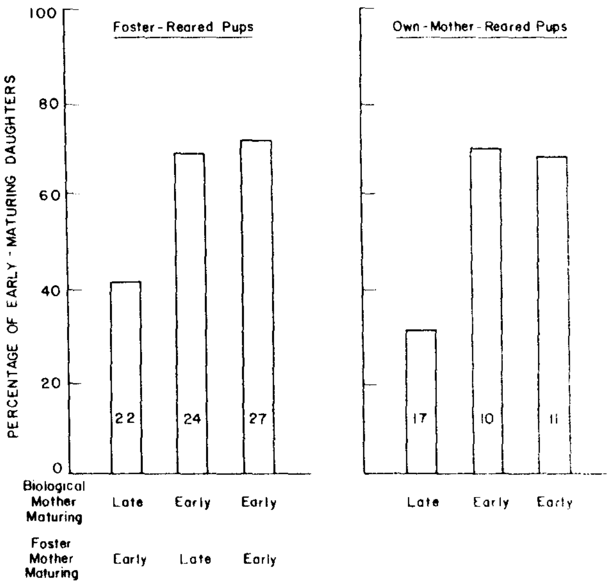

FIG. 5. Percentage of early-maturing daughters raised by early- and late-maturing females. Left-hand panel: Foster-reared pups; Right-hand panel: Pups reared by own mother. Numbers within bars =number of female pups/group.

RESULTS AND DISCUSSION

As was the case in Experiment 1, early-maturing females bred early (mean age at vaginal opening 16.2±1.0 days) gave birth at a significantly earlier age (mean=87.8±4.9 days) than either early-maturing, late-bred (mean=132.9±5.3 days) females (mean age at vaginal opening 16.9±0.7 days) or late-maturing late-bred females (mean age at vaginal opening=38.5±1.4 days; mean age at first parturition 129.2±4.5 days) (both ts>5.92, both ps<0.01).

The percentage of early-maturing daughters in litters produced by early-maturing females bred early was high (64.8%), as was the percentage of early-maturing daughters in litters of early-maturing females bred late (64.3%). Late-maturing females bred late had significantly fewer early-maturing daughters (31.8%) than females in either of the other two groups (both χ^2s>5.11, both ps<0.02). Differences in rate of maturation of daughters born to early- and late-maturing females are not due to differences either in age of mothers or size or sexual composition of their litters.

Nursing and gathering scores were affected by both size and sex-composition of litters and by age of mother. As can be seen in Fig. 3, which presents nursing and gathering scores of females in the three groups, equating size and sex-ratio of litters and altering age of females at parturition had significant effects on both measures of maternal behavior. As in Experiment 1, gathering scores for early-maturing females bred early differed significantly from those of late-maturing females bred late, $t=4.57$, $p<0.01$, and early-maturing females bred late were significantly different in their gathering scores from early-maturing females bred early, $t=3.53$, $p<0.01$. Similarly, nursing scores for early-maturing females bred early differed significantly from those of late-maturing females bred late, $t=3.95$, $p<0.01$. In contrast to the results of Experiment 1, in the present experiment, early-maturing females bred late were significantly different from early-maturing females bred early in their nursing behavior, $t=2.25$, $p<0.05$.

Comparison of the results of the test of nursing behavior in the present experiment with that of Experiment 1 suggests that effects of maternal age interact with litter characteristics to influence nursing behavior. Early-maturing females bred late in Experiment 1, rearing their natural litters, exhibited nursing scores like those of early-maturing females bred early, while, in the present experiment, early-maturing females bred late, nursing only two male and two female pups, exhibited nursing scores like those of late-maturing females bred late.

Figure 4 presents data describing retrieval behavior of subjects in the three groups. As examination of the figure suggests, early-maturing, late-bred females were intermediate between the other two groups in retrieval behavior. They did not differ significantly from either (Fisher's Exact Test, both ps>0.10, one-tailed test). Late-breeding interacted with litter size and litter composition to modify retrieval behavior in early-maturing females.

Considered together, results of Experiments 1 and 2 suggest that differences observed in maternal behaviors (nursing, gathering and retrieval) of early- and late-maturing female gerbils are the result of differences in age at first parturition and/or size and sex-composition of litters. Differences in rate of maturation of daughters in litters born to early- and late-maturing females were resistant to manipulation of these variables.

EXPERIMENT 3

Litters in Experiments 1 and 2 were reared by their natural mothers. In consequence, it was not possible to determine whether observed differences in the rate of maturation of daughters born to early- and late-maturing females were due to postnatal influences exerted by the mother or to hereditary or prenatal influences. In the present experiment, early-maturing and late-maturing females reared foster pups in addition to their own young, allowing determination of effects of postpartum behavior of dams on rate of maturation of females in their litters.

METHOD

Subjects

Seventeen late-maturing and 33 early-maturing females served as subjects. These animals were born and reared in the McMaster colony and placed with a proven male at 25 days of age. By selecting from among a much larger group of parturient females those 50 females giving birth within 24 hr of another female, we were able to meet the procedural conditions described below.

Procedure

On the day of parturition, each subject was given one or two foster pups from the litter of a female giving birth within 24 hr of the subject. Litters of foster mothers were then adjusted so that females in each of the three groups described below reared an average of 5.8 pups: the one or two foster females each received, 1 or 2 females from own litters (depending on availability) and enough own male young to bring litters to an average of 5.8 pups/group. Variability in size and sex-composition of litters at birth prevented a more precise method of composing litters. We were, however, able to equate both mean litter size and mean sex-ratio of litters reared by subjects in each group.

Each subject female was assigned to one of three groups. Seventeen late-maturing females reared female pups (n=22) born to early-maturing females as well as some of their own female pups (n=17). Sixteen early-maturing females reared female pups born to late-maturing females (n=24) in addition to some of their own female young (n=10), and, to control for effects of the fostering manipulation, 17 early-maturing females reared female pups born to other early-maturing females (n=27) in addition to some of their own female young (n=11). Both fostered and naturally reared female pups were examined daily from Day 1 to Day 25 to determine age at vaginal perforation.

RESULTS AND DISCUSSION

The results of Experiment 3 are presented in the two panels of Fig. 5 that show the percentage of early-maturing fostered and natural daughters raised by mothers in each of the three groups. As can be seen in the right-hand panel of Fig. 5, daughters born to and reared by early-maturing mothers (mean age at vaginal opening 15.8±0.5 days) were significantly more likely to exhibit vaginal opening prior to Day 25 than were daughters born to and reared by late-maturing mothers (mean age at vaginal opening 37.6±1.2 days) (Fisher's Exact Tests, both *ps*<0.05).

The main results of Experiment 3 are found in the left-hand panel of Fig. 5. Rate of maturation of foster-reared pups was determined by their biological mother and not by their foster mother. Pups born to late-maturing mothers and reared by early-maturing mothers were significantly less likely to exhibit vaginal opening prior to Day 25 than pups born to early-maturing mothers and foster-reared by late-maturing mothers ($\chi^2>5.26$, $p<0.02$). The difference in rate of maturation of females born to early- and late-maturing females is the result of prenatal rather than postnatal events.

GENERAL DISCUSSION

Results of the present experiments suggest that differences (1) in maternal behavior of early- and late-maturing female gerbils and (2) differences in characteristics of their litters do not have similar causes. Reduced levels of maternal behavior (as measured by gathering, nursing and retrieval) observed in early-maturing females are the result, either singly or in combination, of the relative youth of early-maturing females at first parturition and the large, female biased litters they produce.

Sex-ratios of litters at birth and rate of maturation of daughters are not influenced either by maternal age or size or sexual composition of litters. Events occurring following birth do not appear to be important in determining rate of maturation of daughters. Differences in sex-ratios of litters born to early- and late-maturing females and differences in rate of sexual maturation of daughters must result from differences in genetic material passed on by early- and late-maturing females to their daughters and/or from differences in the uterine environments in which embryos and fetuses of early- and late-maturing females develop.

It has been suggested that the proportion of males in litters is a heritable characteristic in rats [13], possibly mediated by chemical characteristics of cervical fluids influencing relative longevity of X and Y sperm and, consequently, sex-ratios at fertilization [22]. Uterine conditions following fertilization of ova can favor differential survival of either sex [17]. Rate of maturation of daughters, could, similarly be influenced either by hereditary factors and/or by effects of environments experienced by females *in utero* [4, 23, 24, 25]. We are currently exploring effects of differences in genotype and in the uterine environments provided by early and late-maturing gerbils on sex-ratios of litters at birth and rate of maturation of daughters.

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REFERENCES

1. Cheal, M. Lifespan ontogeny of breeding and reproductive success of Mongolian gerbils. *Lab Anim* **17:** 240–245, 1983.
2. Clark, M. M. and B. G. Galef, Jr. Measures of growth, development, and sexual behavior in Mongolian gerbils (*Meriones unguiculatus*): effects of photic period during ontogeny. *Dev Psychobiol* **18:** 191–202, 1985.
3. Clark, M. M., C. A. Spencer and B. G. Galef, Jr. Reproductive life history correlates of early and late sexual maturation in female Mongolian gerbils. *Anim Behav*, in press.
4. Clemens, L. G., B. Gladue and L. Coniglio. Prenatal endogenous androgenic influences on masculine sexual behavior and genital morphology in male and female rats. *Horm Behav* **10:** 40–53, 1978.

5. Cooley, C. L. and J. R. Slonaker. The effects of early and late breeding on the mother and the sex ratio in the albino rat. *Am J Physiol* **72:** 595–613, 1925.
6. Copeman, S. M. and F. G. Parsons. Observations on the sex of mice. Preliminary paper. *Proc R Soc Lond* **73:** 32–48, 1904.
7. Drickamer, L. C. Effect of size and sex ratio of litter on the sexual maturation of female mice. *J Reprod Fertil* **31:** 82–89, 1976.
8. Drickamer, L. C. Selection of age of sexual maturation in mice and the consequences for population regulation. *Behav Neural Biol* **31:** 82–89, 1981.
9. Drickamer, L. C. Mice selected for age of puberty: Reverse selection and reproductive characteristics. *Biol Reprod* **28:** 843–848, 1983.
10. Elwood, R. W. and D. M. Broom. The influence of litter size and parental behaviour on the development of Mongolian gerbil pups. *Anim Behav* **26:** 438–454, 1978.
11. Grota, L. J. and R. A. Ader. Continuous recording of maternal behaviour in female mice. *Anim Behav* **17:** 723–729, 1969.
12. Kennedy, T. G. and J. P. Kennedy. Effects of age and parity on reproduction in young female mice. *J Reprod Fertil* **28:** 77–84, 1972.
13. King, H. D. Studies on inbreeding. III. The effects of inbreeding, with selection, on the sex ratio of the albino rat. *J Exp Zool* **27:** 1–35, 1918.
14. Marston, J. H. The Mongolian gerbil. In: *The UFAW Handbook on the Care and Management of Laboratory Animals*, edited by UFAW. Edinburgh: Churchill Livingston, 1972, pp. 257–268.
15. Moore, C. L. and G. A. Morelli. Mother rats interact differently with male and female offspring. *J Comp Physiol Psychol* **93:** 667–684, 1979.
16. Orlenev, D. P. and S. V. Pereledov. Restoration of the population structure in the clawed jird following artificial population depression. *Ekologiya* **2:** 58–66, 1981. (Available in English translation from Plenum Press as UDC 591.512.)
17. Priestnall, R. Effects of litter size on the behaviour of lactating female mice (*Mus musculus*). *Anim Behav* **20:** 386–394, 1972.
18. Robinson, R. *Genetics of the Norway Rat*. New York: Pergamon Press, 1965.
19. Rugh, R. and M. Wholfromm. The reproductive performance of the laboratory mouse: Maternal age, litter size and sex ratios. *Proc Soc Exp Biol Med* **126:** 685–687, 1967.
20. Schreiber, R. A., L. K. Ferret and D. Holbert. The effects of parity, litter size, season and breeding protocol on the number of DBA/2J Ten mice available for weaning. *Lab Anim Sci* **25:** 602–608, 1975.
21. Seitz, P. F. D. The effects of infantile experience upon adult behavior in animal studies. I. Effects of litter size during infancy upon adult behavior in the rat. *Am J Psychiatry* **110:** 916–917, 1954.
22. Shettles, L. B. Factors influencing sex ratios. *Int J Gynaecol Obstet* **8:** 643–647, 1970.
23. vom Saal, F. S. Variation in phenotype due to random intrauterine positioning of male and female fetuses in rodents. *J Reprod Fertil* **62:** 637–650, 1981.
24. vom Saal, F. S. and F. H. Bronson. In utero proximity of female mouse fetuses to males: Effect on reproductive performance during later life. *Biol Reprod* **19:** 842–855, 1978.
25. vom Saal, F. S. and F. H. Bronson. Sexual characteristics of adult female mice are correlated with their blood testosterone levels during prenatal development. *Science* **208:** 597–599, 1980.
26. Waring, A. and T. Perper. Parental behavior in Mongolian gerbils (*Meriones unguiculatus*). II. Parental interactions. *Anim Behav* **28:** 331–346, 1980.
27. Wilke, E. L., Jr. *Numbers: A Primer of Data Analysis*. Columbus: Charles E. Merrill, 1985.