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Reproductive life history correlates of early and late sexual maturation in female Mongolian gerbils (*Meriones unguiculatus*)

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Abstract. Age at vaginal introitus is bimodally distributed in female domesticated Mongolian gerbils; some exhibit vaginal perforation before eye-opening (day 16), others after weaning (day 25). We found early- and late-maturing female gerbils to differ significantly in reproductive life history. Early-maturing females first reproduced when younger, had more litters, with more young per litter, and consequently had more than twice as many offspring as late-maturing females. In comparison with late-maturing females, early-maturing females gave birth to and weaned a greater proportion of females per litter and a higher proportion of early-maturing daughters per litter. Further, early-maturing females exhibited reduced maternal behaviour; they spent less time nursing their young and retrieved fewer offspring displaced from the nest than late-maturing females. Even under constant laboratory conditions, there were significant, correlated, circannual rhythms in female fecundity, the proportion of males per litter and the proportion of early-maturing daughters per litter. Review of the field literature suggests that wild Mongolian gerbils may exhibit similar variability in reproductive pattern.

Age at vaginal introitus is one of several indices of puberty commonly used as a dependent variable in laboratory studies of sexual development in female rodents. Investigators working with laboratory strains of house mouse (*Mus musculus*) and Norway rat (*Rattus norvegicus*) have expressed reservations as to the usefulness of vaginal introitus as an index of sexual maturation in their subjects (Kennedy & Mitra 1963; Vandenbergh 1967; Vandenbergh et al. 1972). In both rats and mice, age at vaginal perforation has been found to correlate poorly with age at more functionally significant developmental events, such as age at first oestrus, first copulation, or first parturition. Further, age at vaginal perforation predicts little of the subsequent reproductive activity of female rats or mice (Kennedy & Mitra 1963; Drickamer 1983; Hansen et al. 1983).

Previous studies in our laboratory have revealed that females of the domesticated strain of Mongolian gerbil (*Meriones unguiculatus*) available in North America are unusual among laboratory rodents in that gerbil females exhibit a clear bimodality in the age at which they achieve vaginal perforation (Clark & Galef 1985). Within a randomly-mated colony of gerbils maintained in a single colony room, we found both precocious females, exhibiting vaginal perforation before 23 days of age (with a mode at 16 days), and late-developing females that failed to exhibit vaginal opening until after weaning (with a mode at 32 days of age).

In the studies described below, we examine both the reproductive life histories and the parental behaviour of these early- and late-maturing female gerbils. Our results suggest that in Mongolian gerbils, unlike other domesticated strains of laboratory-maintained rodents described in the literature, age at vaginal patency is a useful predictor of life-time reproductive performance.

GENERAL METHODS

Breeding, Rearing and Maintenance

Multiparous pairs of Mongolian gerbils, acquired from Tumblebrook Farms (Brookfield, Massachusetts), served as the source of subjects in all experiments. These breeding pairs were housed in 35 × 30 × 15-cm polypropylene cages that were covered with 1·27 cm (1/2 inch) hardware cloth and carpeted with a thin layer of wood-chip bedding (Betta-chip, Northeastern Products Corporation, Warrensburg, New York). The colony was maintained ad libitum on Purina Laboratory Rodent Chow and water, on a 12:12 h light:dark cycle (light onset 0700 hours) in a single temperature- and humidity-controlled colony room. Breeding pairs were examined daily, and when a female became visibly pregnant (third trimester), her mate was removed from her cage. Cages containing pregnant females were examined twice daily (1000 and 1600 hours) to determine date of parturition.

Pups in each litter were toe-clipped for individual recognition on the day of birth (day 1) and weaned to a cage separate from their dam on day 25. During the period from birth to weaning, all female pups were examined daily to determine their age at vaginal perforation. Examination for vaginal introitus was accomplished by applying gentle pressure just below the vagina. Each female was weighed on the day her vagina was observed to perforate.

On the day of weaning, each female was paired with a 100–140 g male that had previously bred successfully in our colony. Those females that had not exhibited vaginal introitus before weaning, continued to be examined daily until vaginal introitus occurred. Females were left with their respective mates until they were either visibly pregnant, or had reached 210 days of age, whichever occurred first.

EXPERIMENT 1

Experiment 1 consisted of two parts. Study 1 was undertaken (1) to establish the distribution of age and body weight at vaginal introitus in female Mongolian gerbils and (2) to examine the first litters produced by early- and late-maturing females. In study 2, we examined the life-time reproductive histories of early- and late-maturing females.

Methods

Subjects and procedure

Study 1. Ninety female gerbils, selected from 85 litters reared in the McMaster colony (as described in General Methods) served as subjects. These 90 females were used to determine age at vaginal opening, body weight at vaginal opening, age at first parturition, and characteristics of first litters born to early- and late-maturing females.

Study 2. An additional 18 females (nine early- and nine late-maturing) were selected from 18 litters for examination of life-time reproductive histories. Females in study 2 were treated exactly as described in General Methods except: (1) at weaning (day 25), each female was paired with a 25-day-old male rather than with an experienced breeder. This modification in procedure was effective in ensuring that termination of breeding in females did not result from senescence or death of their consorts. (2) Because we were interested in life-time reproduction, breeding pairs were left together until the death of the female.

Results

The main results of study 1 are presented in Figs 1 and 2 and in Table I. Figure 1 presents data describing the distribution of both age and body weight at which vaginal introitus occurred in the 90 females in study 1. There was a clear bimodality in the distribution of both age and body weight at vaginal opening. One subpopulation of 39 females (early-maturing) exhibited vaginal perforation at a mean age of $15{\cdot}9 \pm 0{\cdot}53$ days and a mean body weight of $11{\cdot}9 \pm 0{\cdot}4$ g. The second subpopulation of 51 females (late-maturing) exhibited vaginal perforation at a mean age of $35{\cdot}2 \pm 0{\cdot}71$ days and a mean body weight of $32{\cdot}5 \pm 1{\cdot}24$ g.

Figure 2 presents a cumulative distribution of the age at first parturition of the 32 early- and 36 late-maturing females in study 1 producing a litter before reaching 210 days of age. Early-maturing females reproduced for the first time at an earlier mean age ($\bar{X} = 86{\cdot}1 \pm 2{\cdot}9$ days) than late-maturing females ($\bar{X} = 108{\cdot}5 \pm 5{\cdot}0$ days; two-tailed t-test, $t = 3{\cdot}8$, $df = 66$, $P < 0{\cdot}01$). The proportion of early- and late-maturing females failing to give birth before 210 days of age did not differ significantly ($\chi^2 = 1{\cdot}57$, $df = 1$, $P > 0{\cdot}20$) and the fertility rate for all subjects (75·6%) was within the range usually observed in domesticated gerbil populations (Arrington et al. 1973).

Table I presents data describing characteristics of first litters delivered and reared by early- and late-maturing females in study 1. For purposes of comparison, we have presented similar data describing the first litters delivered and raised by the nine early-maturing and nine late-maturing females in study 2. As can be seen in Table I, in each of two replicates, the first litters raised by early-maturing females were slightly, but not significantly, larger, both at birth and at weaning, than those of late-maturing females. Also, litters born to early-maturing females contained a significantly greater proportion of both females and early-maturing daughters than did litters of late-maturing females.

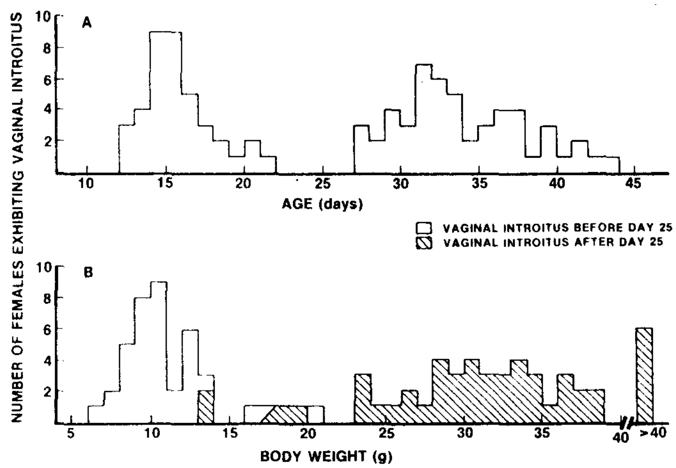

Figure 1. Distributions of (A) ages and (B) body weight of female gerbils at vaginal introitus. Diagonal in B indicates one early- and one late-maturing female.

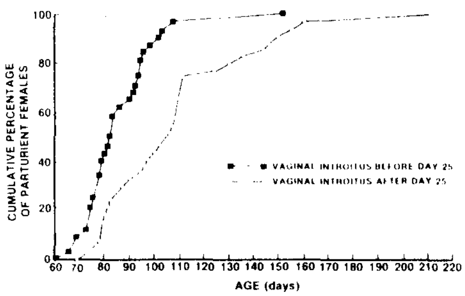

Figure 2. Cumulative percentage of early- and late-maturing females giving birth before day 210 and exhibiting first parturition at various ages.

Table II presents data describing the life-time reproductive histories of the nine early- and nine late-maturing females in study 2. In comparison with late-maturing females, early-maturing females gave birth to significantly more litters, containing slightly more young, resulting in a far greater life-time fecundity for early- than for late-maturing females. Throughout their life-times, early-maturing females delivered and weaned a significantly greater proportion of female pups and produced a significantly higher proportion of daughters exhibiting vaginal perforation before reaching 25 days of age (early-maturing daughters) than late-maturing females.

Table I. Characteristics of first litters produced by early- and late-maturing female gerbils in studies 1 and 2 of experiment 1

	Early-maturing ($N=32$)	Late-maturing ($N=36$)	t	P (two-tailed)
Mean litter size				
Birth	5·7 ± 0·39 (5·8 ± 0·86)	5·4 ± 0·43 (5·6 ± 0·84)	0·59 (0·10)	NS (NS)
Weaning	4·7 ± 0·37 (4·2 ± 0·89)	3·8 ± 0·44 (3·3 ± 1·03)	1·32 (0·70)	NS (NS)
Mean proportion males				
Birth	45·7 ± 4·4 (38·0 ± 8·1)	62·1 ± 3·9 (56·3 ± 6·8)	2·82 (2·21)	*** (*)
Weaning	42·2 ± 4·2 (40·6 ± 6·4)	56·6 ± 4·5 (65·8 ± 5·8)	2·40 (2·98)	** (*)
Mean proportion early-maturing daughters	60·1 ± 5·5 (74·8 ± 14·5)	36·0 ± 7·8 (34·5 ± 12·2)	2·68 (2·17)	*** (*)

Numbers in parentheses refer to the values for females in study 2.
P values are for t-tests: NS = $P > 0·05$; *$P < 0·05$; **$P < 0·02$; ***$P < 0·01$.

Table II. Life-time reproductive history of early- and late-maturing female gerbils

	Early-maturing	Late-maturing	t or μ	P two-tailed
Mean number litters				
Born	5·2 ± 0·84	3·0 ± 0·30	t = 2·62	**
Weaned	4·7 ± 0·89	2·5 ± 0·53	t = 2·46	*
Mean litter size				
Birth	6·0 ± 0·31	5·3 ± 0·58	t = 1·25	NS
Weaning	4·8 ± 0·49	3·2 ± 0·66	t = 1·98	NS
Mean number offspring				
Born	32·7 ± 5·4	17·4 ± 2·7	t = 2·71	**
Weaned	25·1 ± 5·1	11·4 ± 2·8	t = 2·51	*
Mean proportion males/litter				
Birth	40·4 ± 2·24	50·2 ± 4·2	t = 2·18	*
Weaning	39·8 ± 1·6	53·4 ± 6·7	t = 2·43	*
Mean proportion early-maturing daughters/litter	65·1 ± 6·3	41·9 ± 6·5	t = 2·57	*
Mean age first litter (days)	118·7 ± 9·8	161 ± 12·2	t = 2·85	**
Mean age last litter (days)	301·7 ± 37·0	240 ± 18·3	μ = 20	*
Mean life span (days)	325·0 ± 32·6	344 ± 6·4	μ = 27	NS
Mean post-reproductive life span (days)	23·3 ± 12·4	104 ± 22·6	t = 3·51	***

P values: NS = $P > 0·05$; *$P < 0·05$; **$P < 0·02$; ***$P < 0·01$.

As also shown in Table II, early-maturing females both began breeding at an earlier age and continued breeding until a later age than late-maturing females. In spite of their increased reproductive effort, early-maturing females did not show a significantly shorter life-span than late-maturing females (Galef 1983). The post-reproductive period (defined as the time from birth of the last litter to the death of the female) was, however, significantly shorter in early- than late-maturing females.

Comparing the mean age at first parturition of the nine early-maturing females described in Table II, with the distribution of ages at first parturition of the 32 early-maturing females described in Fig. 2 reveals that the nine early-maturing females in study 2 gave birth for the first time at a greater mean age than the early-maturing females in study 1. This was not unexpected. Data presented in Table II describe females paired at weaning with males of their own age, so that their life-time fecundity could be established. Data presented in Fig. 2 describe females in study 1 paired at weaning with sexually mature males. Females described in Table II could not begin reproducing until their consorts achieved sexual maturity, while females described in Fig. 2 could begin to reproduce as soon as they were reproductively capable. Because female gerbils achieve functional sexual maturity at an earlier age than males of their species (Marston 1972; Norris & Adams 1972), one would expect to observe delayed reproduction in early-maturing females paired with juvenile males relative to early-maturing females with mature males.

Discussion

The results of experiment 1 confirm our previous observations of a pronounced bimodality in age at vaginal introitus of female Mongolian gerbils (Clark & Galef 1985). Some females exhibited vaginal perforation before weaning, while others did not do so until 2–3 weeks later, when feeding on solid food was already well established. The present data further indicate that precocious vaginal patency was not the result of a general acceleration of morphological development. Early-maturing females exhibited vaginal opening at lower body weights than late-maturing females; they did not grow more rapidly before achieving vaginal patency. Thus, rate of sexual maturation in female gerbils, as in female mice (Drickamer 1981), appears to be independent of rate of morphological development.

The results of the present studies also indicate that sexually precocious females exhibit very different reproductive profiles from their late-maturing sisters; they began reproducing at an earlier age, continued reproducing to a later age, bore more litters, produced more young, and produced both a greater proportion of female offspring and a greater proportion of early-maturing daughters than late-maturing females.

EXPERIMENT 2

In the course of conducting experiment 1 we noticed marked changes across the year in: (1) the fertility of females, (2) the sex ratios of litters, and (3) the probability of daughters exhibiting precocial vaginal introitus. Because we have been breeding gerbils from the same stock under the conditions described in General Methods for 3 years, we were able to examine, retrospectively, our breeding records for 1982, 1983, and 1984 to look for seasonality both in the sex ratio at birth in 265 litters born to primiparous females during 36 consecutive months and in the proportion of early-maturing daughters in the 207 litters containing females at weaning. Unfortunately, our records were not adequate to permit precise determination of seasonality in fertility because slightly different numbers of animals were bred in different months and incomplete records were kept of females that were paired with a male, but failed to reproduce.

Results

Figure 3A shows the mean percentage of females in each litter born in each month of the year exhibiting vaginal introitus before reaching 25 days of age. Of females born during the summer months (June, July and August), 61–65% matured early, while only 32–36% of females born during the winter months (December, January and February) exhibited early vaginal perforation. Across all 12 months of the year, the mean percentage of early-maturing females per litter varied significantly ($F = 2{\cdot}08$, $df = 11{,}195$, $0{\cdot}01 < P < 0{\cdot}05$).

As can also be seen in Fig. 3, months in which the greatest number of litters were born in our colony were those in which the greatest proportion of females were early-maturing. As indicated above, because of inadequacies in our records, the number of litters born per month is not a precise measure of fecundity. However, the general pattern of low levels of reproductive activity in winter months and high rates of litter production in summer months is consistent both with other observations on domesticated gerbils (Robinson 1975) and with field reports of reproduction in natural habitat (Leont'ev 1954; Benimetskii 1975; Obuhov 1977).

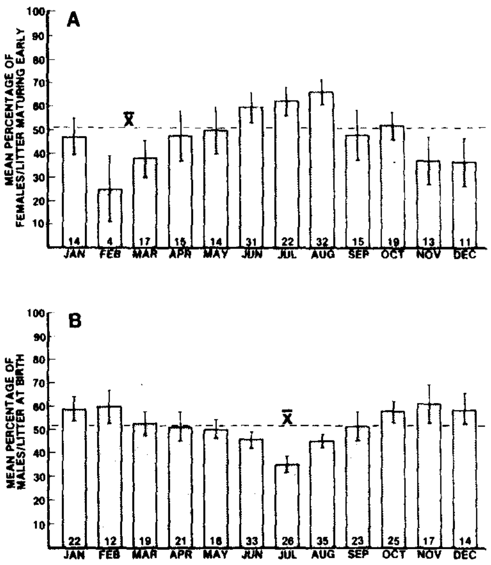

Figure 3. (A) Mean percentage of females/litter exhibiting vaginal introitus prior to reaching 25 days of age. (B) Mean percentage of males/litter at birth. Figures inside bars indicate the number of litters examined in each month. Flags indicate ± 1 SE.

Figure 3B presents data describing the mean sex ratio of litters born during each month of the year. The sex ratio of litters changed seasonally ($F = 1{\cdot}93$, $df = 11{,}253$, $P < 0{\cdot}03$), with the greatest proportion of males per litter being produced during the winter months ($\bar{X} = 59{\cdot}4$) and the smallest during the summer months ($\bar{X} = 42{\cdot}1$). Across the entire year, the mean proportion of males per litter did not differ significantly from 0·50 ($\bar{X} = 50{\cdot}96 \pm 1{\cdot}4\%$).

Month-to-month variation in production of male young was significantly negatively correlated with month-to-month variation in the production of early-maturing daughters ($r = -0{\cdot}78$, $t = 4{\cdot}2$, $P = 0{\cdot}01$). The variation in sex ratio and proportion of early-maturing daughters born in different seasons was not an artefact of changes in the ratio of early- to late-maturing females giving birth in any month. Examination of first litters born to early-

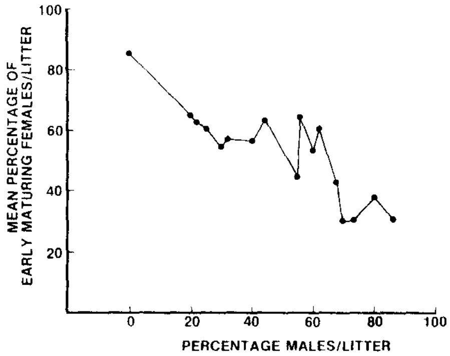

Figure 4. Mean percentage of females/litter exhibiting vaginal introitus before reaching 25 days of age as a function of the percentage of males/litter.

maturing females across 3 years revealed similar significant changes across the four seasons both in the proportion of early-maturing females per litter ($F=2{\cdot}94$; $df=3{,}84$; $P<0{\cdot}05$) and in the sex ratio of litters at birth ($F=4{\cdot}63$; $df=3{,}103$; $P<0{\cdot}01$).

As can be seen in Fig. 4, which shows the mean percentage of females per litter maturing early as a function of the percentage of males per litter, there was a significant negative correlation across all 207 litters between the sex ratio of litters and the percentage of females exhibiting vaginal introitus before reaching 25 days of age ($r=0{\cdot}85$, $t=6{\cdot}4$, $P<0{\cdot}001$). Further, there were significant correlations both between litter size at birth (range 1–10) and the mean percentage of males per litter (Spearman $\rho=-0{\cdot}89$, $P<0{\cdot}02$) and between litter size at weaning (range 1–9) and mean percentage of males per litter (Spearman $\rho=-0{\cdot}90$, $P<0{\cdot}02$).

Mean litter size at birth ($\bar{X}=6{\cdot}0\pm0{\cdot}1$) did not vary seasonally ($F=1{\cdot}65$, $df=11{,}253$; NS), while mean litter size at weaning ($\bar{X}=4{\cdot}3\pm0{\cdot}2$) did ($F=3{\cdot}44$; $df=11{,}253$; $P<0{\cdot}001$). During the summer months (June, July and August) litters averaged $5{\cdot}0\pm0{\cdot}2$ pups per litter at weaning. In the winter (December, January and February), only $3{\cdot}1\pm0{\cdot}4$ pups per litter survived to weaning. We found significant correlations across the 12 months of the year between both mean litter size at birth and percentage of early-maturing daughters per litter ($r=0{\cdot}58$, $t=2{\cdot}26$, $P<0{\cdot}05$) and between mean litter size at weaning and mean percentage of early-maturing daughters per litter ($r=0{\cdot}74$, $t=3{\cdot}49$, $P<0{\cdot}01$).

Discussion

Whether the negative correlation between the proportion of males in a litter at birth and the proportion of early-maturing females per litter reflects an underlying causal relationship remains to be determined. We are currently engaged in analyses of the determinants of rate of sexual maturation in female gerbils. It is surely possible that the presence of males either in utero (vom Saal & Bronson 1980) or in a litter after delivery (Drickamer 1976) might affect rate of sexual development of females.

Whether indicative of causal relationships or not, the existence of strong correlations among the rate of development of females in litters, the proportion of males in litters and the fecundity of females poses problems for the functional interpretation of the observed seasonality in all three characteristics of reproduction. Seasonality in sex ratio, fecundity, or production by early-maturing daughters, might each be an epiphenomenal by-product of mechanisms responsible for one of the other two phenomena. For example, it might be the case that seasonality in the production of early-maturing daughters enhances fitness markedly and is accomplished by seasonal manipulations of sex ratio in utero, which are mildly fitness reducing. Alternatively, seasonal changes in the uterine environment, reducing reproductive effort during unfavourable seasons, might alter both sex ratio at birth and the sexual development of daughters. In any case, correlation among various measures of reproduction requires caution in construction of functional explanations of seasonality in any given index.

Seasonality in age at vaginal introitus, sex ratio of litters, and, obviously, reproductive effort may be fairly common in temperate zone rodents. Like domesticated female Mongolian gerbils, laboratory-maintained female C57BL/10 mice exhibit earlier vaginal opening in summer than in winter (Yoon 1955). Berry & Jacobsen (1971) report a marked seasonality in the sex ratios of wild *Mus musculus* litters at weaning, which might reflect seasonality in sex ratios at birth. We have, however, found no data base in the published literature permitting calculation of correlations among seasonally varying reproductive parameters in other species.

EXPERIMENT 3

In the course of observing female gerbils rear dozens of litters of young, we were struck by apparent differences in the maternal behaviour of early- and late-maturing females. Late-maturing females seemed both to spend more time in contact with their young and to be more willing to retrieve their young when they strayed from the nest. In the present experiment, we formalized these observations.

Method

Subjects

Subjects were the 30 early- and 30 late-maturing primiparous females in study 1 of experiment 1 that bore and successfully weaned young.

Procedure

Nursing and gathering behaviour. The cage of each of the 60 females was examined twice daily (1000 and 1500 hours) from the day of parturition to weaning on day 25 post-partum to determine whether, at the moment of inspection: (1) all pups were gathered in the nest and (2) the dam was in a nursing posture over her pups and the pups were attracted to their dam's nipples. Each female was awarded a score from 0–10 (two inspections × 5 days) to describe (1) her gathering and (2) her nursing behaviour during successive 5-day periods.

Retrieval of pups. Ten early-maturing and 10 late-maturing primiparous females were tested for their response to the displacement of two of their own pups outside the nest on day 10 post-partum. The experimenter simply picked the dam up from the nest by her tail, removed two pups (one male and one female), lowered the dam back on the nest, and put the two pups in the corner of the home-cage diagonally opposite the nest-site. During the 5-min period following displacement of the test pups, the experimenter observed the behaviour of the dam.

Results and Discussion

The main results of experiment 3 are presented in Figs 5 and 6 which describe, respectively, the results of observations of nursing and gathering, and retrieval. As can be seen in Fig. 5, late-maturing females spent more time nursing their pups ($F = 15{\cdot}35$, $df = 1{,}58$, $P < 0{\cdot}01$) and were more likely to keep their young gathered in the nest ($F = 4{\cdot}56$, $df = 1{,}58$, $P < 0{\cdot}05$) than early-maturing females. Similarly (Fig. 6), late-maturing females were more likely to retrieve their pups during a 5-min test

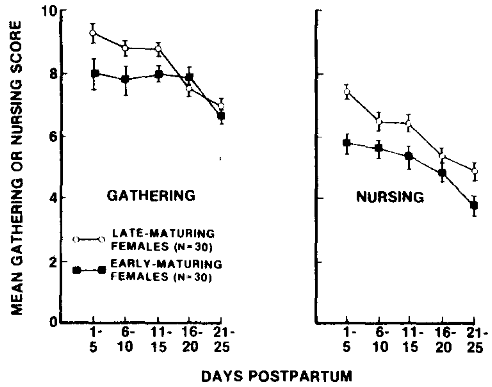

Figure 5. Mean gathering (left-hand panel) and nursing (right-hand panel) scores of early- and late-maturing primiparous gerbils. Flags indicate $\pm$ 1 SE.

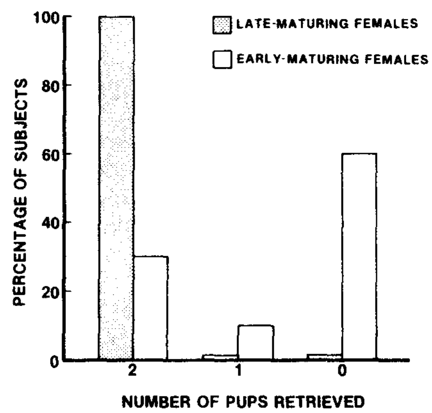

Figure 6. Retrieval of own young by 10-day-post-partum early- and late-maturing primiparous female gerbils.

(Fisher's exact test, $P < 0{\cdot}01$). Even those early-maturing females that did retrieve one or more pups during the 5-min test period retrieved the first pup with considerably longer latency ($\bar{X} = 97{\cdot}5 \pm 30{\cdot}8$ s) than late-maturing females ($\bar{X} = 25{\cdot}8 \pm 9{\cdot}93$ s).

Taken together, the results of the present experiment suggest that early- and late-maturing gerbils differ in their general commitment of time and energy to the care and maintenance of their young.

GENERAL DISCUSSION

The results of the studies described above indicate that, among females of the domesticated strain of Mongolian gerbil available in North America today, two rather different patterns of reproduction exist. Some females exhibit signs of sexual maturation before weaning, others during the post-weaning period. Early-maturing animals began breeding at a relatively early age, continued to breed throughout the remainder of their lives, and produced more than twice as many progeny as late-maturing females. These sexually precocious females also produced a greater proportion of female young and a greater proportion of early-maturing daughters than late-maturing females. In addition, early-maturing females were, at least in terms of the measures of maternal behaviour we employed, less solicitous of their dependent young than late-maturing females. Female gerbils exhibiting early and late vaginal introitus thus appear to differ in many of the reproductive and behavioural characteristics used by Pianka (1970) and others to differentiate r- from K-strategists.

One is naturally led to ask what selective pressures might produce or maintain such differences in reproductive strategy in a population of female gerbils. As mentioned in the discussion of experiment 2, selection may have acted on any or all of three correlated reproductive parameters: rate of maturation of daughters, sex ratio of litters and seasonality of reproductive effort. Because the potential benefits of seasonal reproduction in temperate zones is self-evident, we will not discuss them further here. Instead, we will focus on possible explanations for the observed variability in rate of maturation of females and the sex ratios of litters.

Rate of Sexual Maturation in Females

Artificial selection

Introduction of wild gerbils into relatively sheltered captive environments in 1934 (Ando & Nomura 1956) may have increased the relative reproductive success of those females that reproduced early, often and prodigiously, and minimized their investment in any single litter. In a sheltered environment, any reproductive advantage accruing to females that, in the natural environment, delayed reproduction and invested greater resources in a smaller number of young might well disappear. Hence, the contemporary domesticated strain of gerbil may be in a period of transition from 'obligate relatively K-selected' to 'obligate relatively r-selected' as a consequence of attenuation of environmental demands on mothers in captivity. Consistent with this notion is the fact that reports of age and body weight at vaginal introitus among gerbils during the period close to their introduction into captivity are similar to those of late-maturing females in the present study. For example, Vick & Banks (1969) present a distribution of age at vaginal introitus in 50 female gerbils with a mean at 53·2 days and a range of 41–112 days. Similarly, in 1960, Nakai et al. reported vaginal opening in gerbils occurring at from 40 to 76 days post-partum at an average body weight of 34 g. The absence of evidence of early-maturing females in these older reports suggests that early maturation may be, at least in part, a consequence of subsequent generations of laboratory maintenance.

Natural selection

It is also possible that the variability of the natural environment in which Mongolian gerbils evolved has produced a species in which females are bimorphic along the r–K dimension. Both our laboratory data and field evidence suggest that individual females may be facultative r–K strategists, responding to environmental conditions at the time of reproduction in selecting both the investment to be made in individual young and a bias in reproductive strategy to be imparted to those young.

The Mongolian steppe, the natural habitat of *M. unguiculatus* (Fetisov & Moskovskiy 1948; Leont'ev 1954) is an area of climatic extremes. Winters are harsh, gerbil populations are dependent on food hoards for sustenance, and reproductive rates fall. Across much of the species range, summers are rainy and hot (Ochirov & Bashanov 1975), gerbil populations explode in numbers, and out-migrants from established populations are common (Leont'ev 1954, 1962). Hence in spring and early summer, one might expect selection to favour production of large numbers of early-maturing females, while in fall and early winter, females producing smaller numbers of late-maturing over-wintering females might be more successful.

There are two peaks in breeding activity among gerbils in the field, a large one in May–June and a smaller one in August–September (Leont'ev 1954). Individual females may be active during both breeding periods (Fetisov & Moskovskiy 1948; Krylova 1978) and it might well be useful to them to be able to bias the reproductive strategy of their young to take into account the season in which those young are born. The data in Fig. 5 suggest that such seasonal adjustment in reproductive strategy occurs.

Some field evidence of flexibility in reproductive strategy is also available. Orlenev & Pereladov (1981) artifically reduced the density of a colony of free-living gerbils by poisoning 88% of its members. One month after poisoning, they found a dramatic drop in the weight of pregnant females from a pre-poisoning minimum of 58 g to post-poisoning values in the range of 35–50 g (see also Krylova 1978). The evidence suggests that the capacity for facultative early maturation may well be the result of natural rather than artificial selection.

The fact that early laboratory workers with Mongolian gerbils did not observe early sexual maturation, while it is common today, suggests that generations of breeding under laboratory conditions may have resulted in a change in the conditions sufficient to elicit production of early-maturing daughters. That is, artificial selection may have acted to alter the releasers of a naturally evolved facultative r-strategy rather than to produce the capacity for relatively early maturation and its reproductive correlates.

Sex Ratios of Litters

As discussed in experiment 2 above, it is possible that the variation in production of early- and late-maturing females is a by-product of alterations in the sex ratio of litters. Werren & Charnov (1978) have proposed a model which predicts that, in species in which there is both variation in the life history expectations of individuals born at different times of the year and some overlap in generations, selection can favour seasonal shifts in sex ratio. Such a model may apply to free-living populations of Mongolian gerbils. According to Krylova (1978), wild male Mongolian gerbils take 6–8 months to mature and continue to breed until they die, often at 2–3 years of age. Females breed only in mid and late summer in their first year and spring and early summer in their second. Thus, males born in the fall, maturing sexually in spring, would have access during their first breeding season to two generations of breeding females. Those males born in spring and maturing in late summer, would have access only to females of the current year. One might, therefore, expect female gerbils in the wild to produce more male offspring in fall than in spring, as our laboratory-maintained females do.

Although in the absence of adequate field data the selective pressures responsible for the evolution of the phenomena described in the present paper must remain objects of speculation, the phenomena themselves are clear cut. At least under laboratory conditions, female gerbils exhibit seasonal variability in the sex ratios of their litters, the rate of maturation of their daughters and the reproductive patterns their daughters will exhibit throughout life.

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REFERENCES

Ando, K. & Nomura, T. 1956. The status of laboratory animals. In: *Methods of Animal Experimentation in Medical Research* (Ed. by K. Ando & Y. Tajimal), pp. 16–34. Tokyo: Asakurak (in Japanese).

Arrington, L. R., Beaty, T. C., Jr & Kelley, K. C. 1973. Growth, longevity, and reproductive life of the Mongolian gerbil. *Lab. Anim. Sci.*, **23,** 262–265.

Benimetskii, Y. S. 1975. Seasonal changes in the relative weight of the adrenals and gonads in the Mongolian gerbil. *Ekologiya*, **2,** 95–96. (Available in English translation from Plenum Press, New York as UDC 612. 014.)

Berry, R. J. & Jakobson, M. E. 1971. Life and death in an island population of the house mouse. *Exp. Geront.*, **6,** 187–197.

Clark, M. M. & Galef, B. G., Jr. 1985. Measures of growth, development, and sexual maturation in Mongolian gerbils (*Meriones unguiculatus*): effects of photoperiod during ontogeny. *Devl Psychobiol.*, **18,** 191–202.

Drickamer, L. C. 1976. Effect of size and sex ratio of litter on the sexual maturation of female mice. *J. Reprod. Fert.*, **46,** 369–374.

Drickamer, L. C. 1981. Selection for age of sexual maturation in mice and the consequences for population regulation. *Behav. Neur. Biol.*, **31,** 82–89.

Drickamer, L. C. 1983. Mice selected for age of puberty: reverse selection and reproductive characteristics. *Biol. Reprod.*, **28,** 843–848.

Fetisov, A. S. & Moskovskiy, A. A. 1948. Kogtistaya peschanka (*Pallasiomys unguiculatus* M-Edw) v Zabaikal'e. (Clawed jirds in Transbaikal.) *Tr. Irkutsk. Gos. Univ. Im A.A. Zhadnova; Ser. Biol.*, **3,** 1–10.

Galef, B. G., Jr. 1983. Costs and benefits of mammalian reproduction. In: *Symbiosis in Parent offspring Interaction* (Ed. by L. A. Rosenblum & H. Moltz), pp. 249 278. New York: Plenum Press.

Hansen, P. J., Schillo, K. K., Hinshelwood, M. M. & Hauser, E. R. 1983. Body composition at vaginal opening in mice as influenced by food intake and photoperiod: test of critical body weight and composition hypotheses for puberty onset. *Biol. Reprod.*, **29,** 924-931.

Kennedy, G. C. & Mitra, J. 1963. Body weight and food intake as initiating factors for puberty in the rat. *J. Physiol.*, **166,** 408 418.

Krylova, T. V. 1978. Vorastnaya struktura priodioy poputskii Mongol' skoi peschanki (*Meriones unguiculatus*). (Age structure of a natural population of the Mongolian jird.) *Zool. Zh.*, **57,** 1842 1847.

Leont'ev, A. N. 1954. K ekologii kogtistoi peschanki v Buryat Mongol'skoi. (Ecology of the clawed jird in Buryat Mongolia.) *Izvest. Irkutsk. Nauchn-Issled Protivochumnogo Inst. Sibiri Dal'nogo Vost.*, **12,** 137–149.

Leont'ev, A. N. 1962. K izucheniyu populyatsii Mongol'skikh peschanok methodom mecheniya. (Studying a population of Mongolian jirds by the method of marking.) *Izvest. Irkutsk Nauchn-Issled Protivochumnogo Inst. Sibiri Dal'nogo Vost.*, **24,** 296 302.

Marston, J. N. 1972. The Mongolian gerbil. In: *The U.F.A.W. Handbook on the Care and Management of Laboratory Animals* (Ed. by C. W. Hume), pp. 257-268. Edinburgh: Churchill Livingstone.

Nakai, K., Nimura, H., Tamura, M., Shimizu, S. & Nishimura, H. 1960. Reproduction and postnatal development of colony bred *Meriones unguiculatus kurauchii*, Mori. *Bull. Exp. Anim., Tokyo*, **9,** 157 159. (Japanese with English summary.)

Norris, M. L. & Adams, C. E. 1972. Aggressive behaviour and reproduction in the Mongolian gerbil, *Meriones unguiculatus*, relative to age and sexual experience at pairing. *J. Reprod. Fert.*, **31,** 447 450.

Obuhov, P. A. 1977. Peschanki yugo-zapadnoi Tuvy. (Gerbils of south-western Tuva.) In: *Ekologiya i Meditshinskoe Znachenia Peschanok Fauny S.S.S.R.* (Ed. by V. E. Sokolov), pp. 155–157. Moscow: Nauka.

Ochirov, Y. D. & Bashanov, K. A. 1975. *Mlekopitauschie Tuvy.* Kyzyl: Tuvinskoe Knizhnoe.

Orlenev, D. P. & Pereladov, S. V. 1981. Restoration of the population structure in the clawed jird following artificial population depression. *Ekologiya*, **2,** 58–66. (Available in English translation from Plenum Press, New York as UDC 591.512.)

Pianka, E. R. 1970. On r- and K-selection. *Am. Nat.*, **104,** 592 597.

Robinson, D. G., Jr. 1975. Gerbil care and maintenance. *Gerb. Dig.*, **2,** 1 4.

vom Saal, F. S. & Bronson, F. H. 1980. Sexual characteristics of adult female mice are correlated with their blood testosterone levels during prenatal development. *Science, N.Y.*, **208,** 597–599.

Vandenbergh, J. G. 1967. Effects of the presence of a male on the sexual maturation of female mice. *Endocrinology*, **81,** 345-349.

Vandenbergh, J. G., Drickamer, L. C. & Colby, D. R. 1972. Social and dietary factors in the sexual maturation of female mice. *J. Reprod. Fert.*, **28,** 397-405.

Vick, H. & Banks, E. M. 1969. The estrous cycle and related behavior in the Mongolian gerbil *Meriones unguiculatus* Milne-Edwards. *Comm. Behav. Biol.*, **3,** 117-124.

Werren, J. H. & Charnov, E. L. 1978. Facultative sex ratios and population dynamics. *Nature, Lond.*, **272,** 349-350.

Yoon, C. H. 1955. Homeostasis associated with heterozygosity in the genetics of vaginal opening in the house mouse. *Genetics*, **40,** 297-309.

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