

Socially Induced Delayed Reproduction in Female Mongolian Gerbils (*Meriones unguiculatus*): Is There Anything Special About Dominant Females?

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In 4 experiments, the authors explored effects of interaction with both sexually active adult female and unfamiliar adult male Mongolian gerbils (*Meriones unguiculatus*) on young female gerbils' ages at first parturition. Presence of a natural mother retarded development of her daughters. However, presence of a natural mother had no greater effect on her daughters' development than did presence of any other familiar animal, either male or female. Further, exposing young female gerbils to an unfamiliar male accelerated their development even when their reproductively active mothers were present. The data indicate that maintaining young female gerbils in stable family groups results in both inhibition of sexual maturation (caused by exposure to familiar individuals) and failure to activate sexual development (caused by lack of exposure to unfamiliar males).

Often only 1 of several females in a rodent family delivers most or all of the young that the family produces. Other female family members either do not reproduce at all or show significant delay in the onset of reproductive activity (Gudermuth, Butler, & Johnston, 1992). Such skewed reproduction in females is frequently interpreted as resulting from reproductive suppression of subordinate females by more dominant individuals of the same sex (e.g., Batzli, Getz, & Hurley, 1977; Bennett, Jarvis, Millar, Sasano, & Ntshinga, 1994; Brant, Schwab, Vandenberg, Schaefer, & Solomon, 1998; Gubernick & Nordby, 1992; Reeve, Emlen, & Keller, 1998; Swanson, 1983; Wasser & Barash, 1983). However, in many species, convincing evidence of suppression of subordinate females' reproduction by dominant females is not available.

Results of previous studies of Mongolian gerbils, the subject species in the experiments described here, indicate that in intact gerbil families (a) the mother of a litter is more likely to bear young than are her daughters, and (b) the age of daughters at first parturition is significantly greater in the presence of a mother than in her absence (Agren, 1984; Clark & Galef, 2001; Payman & Swanson, 1980; Swanson & Lockley, 1978).

This failure to reproduce, seen in many young female members of intact families of gerbils, is unlikely to be a laboratory artifact.

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Natural burrows of Mongolian gerbils are often inhabited by a combination of adults, subadults, and juveniles (Bannikov, 1954; Fetisov & Moskovskiy, 1948; Leont'ev, 1954, 1962). Frequently, only 1 adult female in a group taken from a natural burrow is reproductively active (Agren, Zhou, & Zhong, 1989; Gromov, 1981). Such skew in reproduction suggests that in the field, as in captivity (e.g., Agren, 1976; Clark & Galef, 2001; French, 1994; Payman & Swanson, 1980), reproduction is inhibited or delayed in many female gerbils living in social groups.

As in other mammals, results of laboratory studies of reproduction by female members of families of Mongolian gerbils have been interpreted as indicating that dominant females suppress their subordinates' reproduction. For example, Swanson and Lockley (1978) found that after they removed the mother of a family of gerbils from an enclosure, her daughters' scent glands developed rapidly. It is not surprising that these authors proposed that some stimulus emitted by the mother had inhibited the development of daughters' reproductive systems. However, as noted in Swanson (1983), Swanson and Lockley (1978) could not discover the relevant stimulus, leaving open the question of whether mothers actually produce such a stimulus.

In a more recent study of reproductive development in female Mongolian gerbils, we found evidence that interaction with either a foster mother or with sisters resulted in delayed reproduction in female Mongolian gerbils (Clark & Galef, 2001). Daughters kept with their foster mothers and fathers delivered their first litters at a later age than did daughters kept with their fathers alone, and as the number of sisters kept together with their father and mother became greater, the less likely were any of the sisters to reproduce. In the extreme case, when foster mothers and fathers were housed with 3 sisters from birth, essentially none of the sisters reproduced before reaching 116 days of age, although their foster mother continued to bear offspring (Clark & Galef, 2001).

In the experiments presented here, we continued our examination of causes of reproductive delay in young female Mongolian gerbils. In Experiment 1, we repeated a previous experiment (using

as subjects natural families rather than the foster families that served as subjects in our previous research) and again observed that young female Mongolian gerbils living with both father and mother reproduce more slowly than do female gerbils living with only their father (Clark & Galef, 2001). We undertook Experiment 2 to determine whether a reproductively active female had any special potency in delaying her daughter's reproduction or whether the presence of any familiar individual in a group of gerbils had equivalent effects on the rate of maturation of young female members of that group. In Experiment 3, we placed pubescent female gerbils with intact breeding pairs and compared the strength of retarding effects of interaction with a dominant female with the accelerating effects of interaction with an unfamiliar male. Finally, in Experiment 4, we investigated the effects on the reproductive development of young female gerbils of exposing them to unfamiliar adult males, and we examined the ability of mothers to inhibit such male-accelerated reproductive development. In the General Discussion, we provide a view of reproductive delay in female Mongolian gerbils that focuses on lack of adequate stimulation to promote reproductive development rather than suppression of such development by dominant females.

General Method

Subjects

Litters of Mongolian gerbils (*Meriones unguiculatus*) and their natural parents participated in the experiments. All subjects were third or fourth generation descendants of breeding stock acquired from Charles River Breeding Farms (Wilmington, MA), and all were born and reared in the vivarium of the McMaster University Psychology Department. The colony occupied 100–120 cages in a single temperature- and humidity-controlled colony room illuminated on a 12-hr light–dark cycle. Throughout life, all subjects had ad-lib access to Purina Rodent Laboratory Chow 5001 and water.

Rearing Conditions

Each breeding pair resided in a polycarbonate cage measuring 30 cm × 15 cm × 18 cm. The top of the cage was closed with a lid constructed of wire rods, and its floor was carpeted with a thin layer of wood-chip bedding. When a female became obviously pregnant (in her third week of gestation), she received 5 g of cotton batting with which to build a nest.

Procedure

We recorded the day of birth of each litter, and on Day 32 postpartum, the age at which we regularly wean gerbils in our colony, we removed all but 1 litter member, leaving each adult pair with a single female offspring. Any litters conceived by adult females during postpartum estrus were removed on the day of their birth.

The composition of the various family groups examined in Experiments 1, 2, and 3 is shown in Table 1. In general, as can be seen in the table, groups consisted of 1 juvenile female and either 1 or 2 other animals.

If an adult female family member failed to become pregnant as a result of mating during her postpartum estrus (which occurred only four times in the four experiments described below), we discarded data from her litter. We were interested in the reproductive development of daughters, and if an adult female did not conceive, we could not know whether any failure of young females to become pregnant was caused by a male's lack of potency.

Table 1
Assignment of Subjects to Groups in Experiments 1, 2, and 3

Condition	N	Adult female	Males	Juvenile female
Experiment 1				
Intact family	15	Mother	Father	1 daughter
Father alone	15		Father	1 daughter
Experiment 2				
Ovx female	15	Ovx mother	Father	1 daughter
Gonadx male	15		Father and gonadx male	1 daughter
Brother	10		2 brothers	1 sister
Experiment 3				
Day 1	15	Foster dam	Foster dad	1 female
Day 32	15	Foster dam	Foster dad	1 female

Note. Ovx = ovariectomized; Gonadx = gonadectomized.

Parents and offspring remained undisturbed, except for daily inspection, removal of any litters conceived by adult females during postpartum estrus, and biweekly cage cleaning, until the daughter in each cage either became visibly pregnant or reached 116 days of age without delivering a litter. We chose 116 days postpartum as the age at which to terminate our studies because they had to terminate sometime, and because records kept in our breeding colony indicated that by 116 days of age 90% of females paired with proven males at weaning had delivered their first litters. In our colony, all female gerbils exhibit vaginal introitus before reaching 45 days of age (Clark, Spencer, & Galef, 1986), and gestation in the species lasts 25–26 days.

To prevent litter cannibalism, when a daughter became visibly pregnant, we removed her from the cage that she shared with her parents and placed her in a separate cage.

We determined both the percent of daughters assigned to each condition that gave birth before reaching 116 days of age and the mean age at parturition of those daughters.

Experiment 1: Effects of a Dam on Reproduction by Her Daughters

In Experiment 1, we provide evidence that in female Mongolian gerbils, as in other rodent species examined to date (e.g., Gubernick & Nordby, 1992; Haigh, 1983; Skryja, 1978), daughters housed after weaning with both their dam and father reproduce more slowly than daughters housed with their fathers alone. We conducted Experiments 1 and 2 simultaneously, randomly assigning subjects across conditions, so statistical comparisons of outcomes of the two experiments are appropriate. The experiments are discussed separately solely to simplify the exposition.

Method

Subjects

Thirty breeding pairs of Mongolian gerbils (*M. unguiculatus*) served as subjects in Experiment 1.

Procedure

Half the pairs were assigned to an intact-family condition, and the other half were assigned to a father-alone condition. We treated the 15 families assigned to the intact-family condition exactly as described in General Method. The 15 families assigned to the father-alone condition were treated the same as those assigned to the intact-family condition except that when daughters of families assigned to the father-alone condition were 32 days old, we removed their mothers from their cages.

Results and Discussion

The left panel of Figure 1 shows both the percentages of daughters assigned to father-alone and intact-pair conditions that delivered litters before reaching 116 days of age and the mean ages at which females giving birth before reaching 116 days of age gave birth to their first litters. As can be seen in Figure 1, although mothers' presences had no effect on the probability that daughters would become pregnant, $\chi^2(1, N = 30) = 0.70, ns$, mothers' presences did significantly affect the age at which daughters delivered their first litters, $t(18) = 4.50, p < .01$, delaying daughters' mean dates of parturition by just over 14 days. This finding repeats in natural families our previous finding in Mongolian gerbil foster families that the presence of a dam does not affect the probability that a daughter will become pregnant but does affect the age at which a daughter's first parturition takes place (Clark & Galef, 2001).

Experiment 2: Is There Anything Special About a Mother?

The fact that a mother's presence slows the occurrence of reproduction in her daughters has led many to assume that it is a female's role as mother to her offspring that allows her to delay her daughters' reproduction, even when no direct test of that hypothesis has been made (e.g., Brant et al., 1998; Solomon & Gelz, 1997). In Experiment 2, we determined (a) whether the presence of a reproductively active natural mother in a cage with an adult male and young female was necessary to produce retardation of the

young female's reproductive development, or (b) whether the presence of any other familiar individual would have a similar effect.

Method

Subjects

Forty breeding pairs of Mongolian gerbils (*M. unguiculatus*), 1 daughter born to each pair, 20 brothers of 10 of the female pups, and 15 females born on the same day as each of 15 of the litters delivered by female members of breeding pairs served as subjects in Experiment 2.

Procedure

We used the same procedure in Experiment 2 as that described in the General Method with the following exceptions.

Ovariectomized-mother condition. Young female subjects assigned to this condition were exposed to their mothers in an anovulatory state to determine whether the mothers' reproductive state influenced the development of their daughters. On Day 44 postpartum, we anesthetized the female members of pairs assigned to this condition ($N = 15$) by intraperitoneal injection with sodium pentobarbital (50 mg/kg) and surgically removed their ovaries before returning them to the cage with their daughter and mate.

Gonadectomized-male condition. Young females assigned to this condition ($N = 15$) provided information on the importance of the sex of their respective fathers' adult partners in retarding reproductive development. We created 15 trios, each consisting of one female and 2 male 40-day-old gerbils, gonadectomized 1 of the males, and then waited for the female member of each trio to give birth. On Day 32 postpartum, we removed the mother of the litter that the trio had reared. This left a single 32-day-old female and 2 adult males: 1 the 32-day-old female's father and the other the castrated male. Both of these males had been present throughout the first 32 days of the young female's life.

Brothers condition. Females assigned to this condition ($N = 10$), similar to females assigned to the gonadectomized-male condition, provided information on the importance of a female presence in inhibiting reproduction. On Day 32 postpartum, we removed both adults and all juveniles except for two males and one female from the litters assigned to this condition.

Results and Discussion

The main results of Experiment 2 are presented in the right panel of Figure 1. As is clear from examination of the figure and as statistical tests confirmed, there were no significant differences among groups in the percentages of daughters giving birth before reaching 116 days of age, $\chi^2(4, N = 70) = 3.29, ns$, and only the father-alone group differed from other groups in mean age at parturition of those daughters that gave birth before reaching 116 days of age, $F(4, 65) = 3.16, p < .02$. Ovariectomized females, gonadectomized adult males, and juvenile males were each as effective in retarding young females' reproductive development as were young females' own mothers. This result suggests that interaction with any familiar individual, regardless of that individual's age, sex, or reproductive condition, delays reproductive development in female Mongolian gerbils. These findings are also consistent with our previous results showing that sisters, similar to mothers, inhibit a young female gerbil's reproduction (Clark & Galef, 2001).

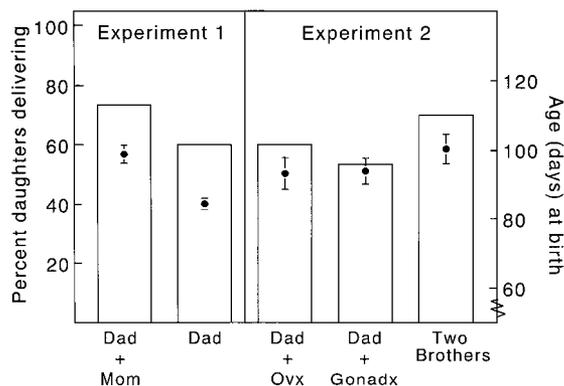


Figure 1. Data from Experiments 1 (left) and 2 (right). Bars represent the percentages of cages in which the young female delivered a litter before reaching 116 days of age, and points represent the mean ages at parturition of females that delivered a litter before reaching 116 days of age. Error bars represent plus or minus one standard error of the mean. Ovx = ovariectomized; Gonadx = gonadectomized.

Experiment 3: Effects of Age at Fostering

To support the hypothesis that interaction with an older, dominant, reproductively active female retards reproductive development of younger females, we would expect a foster daughter introduced at puberty into an enclosure with a breeding pair to reproduce at a relatively late date. If, in addition, exposure to an unfamiliar adult male accelerates reproductive development, then placing a 32-day-old female with an established breeding pair should accelerate her rate of maturation. In the present experiment, we compared ages at first parturition of single foster daughters placed with intact breeding pairs on either Day 1 or Day 32 postpartum.

Method

Subjects

Thirty breeding pairs of Mongolian gerbils (*M. unguiculatus*) and 30 female gerbils born on the same day as litters born to the breeding pairs served as subjects.

Procedure

The procedure was that described in General Method except that (a) we removed the litters of 15 females on the day of their birth and replaced them with a foster litter born on that day, and on Day 32 postpartum we removed all but 1 female foster pup (Day 1 condition), and (b) on Day 32 postpartum, we removed the litters of the remaining 15 females when they were 32 days old and replaced them with a single foster pup of the same age (Day 32 condition).

Results and Discussion

The results of Experiment 3 are presented in Figure 2. As can be seen in the figure, placing a foster pup with a breeding pair at puberty had no effect on probability of reproduction (*ns*) and significantly accelerated reproductive maturation in young females, $t(28) = 2.38, p < .03$. It is clear that stimulative effects of interaction with an adult male were more potent than any retardant effects of interaction with an older, reproductively active female.

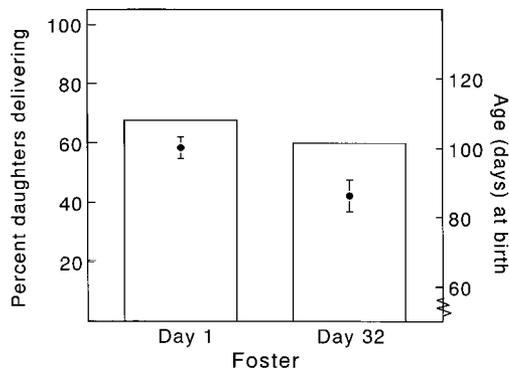


Figure 2. Data from Experiment 3. Bars represent the percentages of cages in which the young female delivered a litter before reaching 116 days of age, and points represent the mean ages at parturition of females that delivered a litter before reaching 116 days of age. Error bars represent plus or minus one standard error of the mean.

Experiment 4: Effects of an Unfamiliar Male

In the present experiment, we further examined both the role of exposure to an unfamiliar adult male gerbil in stimulating reproductive development in conspecific females and the ability of mothers to inhibit reproduction by daughters exposed to an unfamiliar male. We have found previously (Clark & Galef, 2001) that when 3 sisters are left from birth with foster parents, sisters rarely deliver young by the time they reach 116 days of age.

Here, we both repeated that observation and introduced a strange male into cages containing a foster dam and 3 sisters. If exposure to a strange male overrides the inhibition on reproduction imposed by familiar individuals, then one would expect daughters exposed to an unfamiliar male to reproduce at an early age even in the presence of several familiar females.

Method

Subjects

Thirty-nine families of gerbils served as subjects. Thirteen of these families consisted of a foster pair and 3 sisters that they reared from birth. In 13 of the remaining 26 families, the foster father was replaced with an unfamiliar male when the young females were 32 days old. In the last 13 families, we placed 4 sisters with an unfamiliar adult male when the sisters reached 32 days of age. Thus, all groups contained 4 females and 1 male, but they differed in whether the male was familiar or unfamiliar to the females and whether a reproductively active, sexually mature female was present in a group.

To prevent unnecessary aggression, for the first 24 hr that an unfamiliar male was in a cage we separated the male from the females by a screen partition. During this 24-hr period, the male and females could become habituated to one another but could not fight.

Procedure

We examined all females daily for signs of pregnancy until 1 young female subject in a cage became pregnant or the young females in a cage were 116 days old, whichever occurred first. We again removed pregnant females to separate cages and determined the date of parturition.

Results and Discussion

The main results of Experiment 4 are presented in Figure 3. Inspection of the figure reveals, as we have reported previously (Clark & Galef, 2001), that when 3 daughters are left with their foster parents, they rarely deliver litters before reaching 116 days of age. The figure also shows that introduction of an unfamiliar male into a cage containing either a foster mother and 3 sisters or 4 sisters causes a significant increase in the percentage of females breeding, $\chi^2(2, N = 39) = 31.8, p < .001$. The presence of a reproductively active female had no effect on the age at reproduction induced by an unfamiliar male, $t(22) = 0.75, ns$, or in the probability of reproduction by a young female. Mongolian gerbils are thus unlike pine voles (*Microtus pinetorum*), in which reproductive activation of females fails to occur following introduction of a novel male (Schadler, 1990), or house mice (*Mus domesticus*), in which effects of females override accelerating effects of novel males (Drickamer, 1982).

General Discussion

Taken together, the results of the present experiments provide little support for the hypothesis that mothers, other reproductively

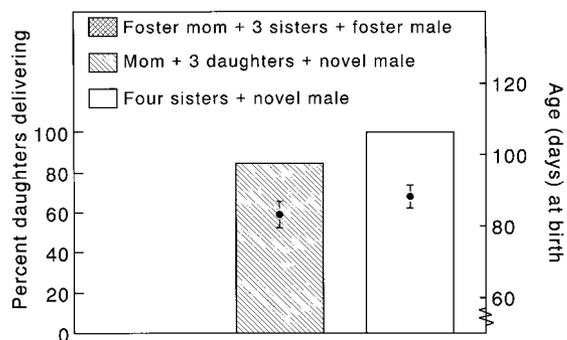


Figure 3. Data from Experiment 4. Bars represent the percentages of cages in which 1 or more young females delivered a litter before reaching 116 days of age, and points represent the mean ages at parturition of females that delivered a litter before reaching 116 days of age. No daughters delivered in cages with a foster mother, 3 sisters, and a foster male. Error bars represent plus or minus one standard error of the mean.

active females, or dominant older females play any special role in delaying reproductive maturation of young female Mongolian gerbils. Foster mothers, ovariectomized females, castrated males, young males, and young females (Clark & Galef, 2001) were as effective as were young females' own reproductively active mothers in delaying the onset of reproduction in young female gerbils with whom they lived.

In interpreting our previous finding (Clark & Galef, 2001) that as the number of sisters in a cage with a foster father became greater, fewer of the sisters reproduced (Clark & Galef, 2001), we proposed that sisters inhibited one another's reproduction. In interpreting the further observation that this mutual inhibition among sisters increased when a reproductively active foster mother was present (Clark & Galef, 2001), we concluded that the inhibition sisters exert on one another's development was greater when they were also exposed to an older, reproductively active female. Given the results of Experiments 1 and 2, in which reproductively active females were shown to have no special ability to inhibit reproduction in young females, it now seems more reasonable to propose that (a) interaction with familiar individuals, regardless of their sex or reproductive status, delays sexual maturation in young female gerbils; and (b) increasing the number of familiar individuals to which a young female is exposed has a cumulative effect.

Findings in Experiments 3 and 4 in the present series indicate that reproductive development of female Mongolian gerbils living in their natal social groups may be unactivated as well as inhibited. Stimulation provided by interaction with an unfamiliar male was sufficient to bring young female gerbils into a reproductive condition, even when a dominant, reproductively active mother was present. Such acceleration of reproduction in young females living with both mother and sisters produced by introduction of an unfamiliar male suggests that lack of activation may be more important than inhibition in determining age at first parturition of young female gerbils.

In some other mammalian species, as in Mongolian gerbils, placing an unfamiliar adult male in an established group has proven at least as effective in inducing young females to breed as has removal of the breeding female (e.g., common mole-rats [*Cryptomys* sp.], Burda, 1995; prairie voles [*Microtus ochro-*

gaster], Carter, Getz, Gavish, McDermott, & Arnold, 1980; white-footed mice [*Peromyscus leucopus*], Haigh, 1987; cotton-top tamarins [*Saguinus oedipus*], Widowski, Ziegler, Elowson, & Snowdon, 1990; Ziegler, Savage, Scheffler, & Snowdon, 1987). The present data, together with those from other species, suggest that inbreeding avoidance may be more important and reproductive suppression by a dominant older female less important in determining age at first reproduction in female mammals than is generally supposed.

The importance of exposure to unfamiliar males in acceleration of puberty in several rodent species suggests that the decline in age at menarche observed in women in recent decades (Tanner, 1962) may be a result of stimulative effects of increased exposure of young women to unfamiliar men rather than their decreased exposure to various inhibitory stimuli (Burger & Gochfeld, 1985; Surbey, 1990). Increasing frequencies of remarriage and consequent introduction of an unfamiliar man into the family unit as well as increased exposure of young women to unfamiliar men in schools and other social settings may be a cause of accelerated rates of sexual development in women analogous to those we have found in young, female Mongolian gerbils.

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