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Socially induced infertility: familial effects on reproductive development of female Mongolian gerbils

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We examined social influences on age at first reproduction in female members of 240 litters of Mongolian gerbils, *Meriones unguiculatus*. The results indicated that: (1) sisters inhibit one another's reproductive development, although this mutual inhibition is more strongly expressed in the presence than in the absence of an older, reproductively active female, (2) either sexual incompatibility develops between male gerbils and females that they help to rear, or female gerbils need to be exposed to strange males in order for their reproductive development to proceed to sexual maturity, (3) exposure of adult males to young females increases the males' subsequent latency to impregnate females other than those to which the males were exposed. Taken together the results suggest that age at first impregnation of female Mongolian gerbils living in family groups can be influenced by interactions with their sisters, dam and father, as well as with unfamiliar males.

In many group-living rodent species, a single female in each group produces most or all of the young, and reproduction by other female group members is either delayed or permanently prevented (Keane et al. 1994; Burda 1995; Faulkes & Abbott 1997; Brant et al. 1998; for review, see Solomon & Getz 1997). In Mongolian gerbils, *Meriones unguiculatus*, the subject species in the present experiment, it has been shown repeatedly in the laboratory that a founding female is far more likely to reproduce than her daughters (Swanson & Lockley 1978; Payman & Swanson 1980; Agren 1981, 1984; French 1994). Often, the ovaries of adult, nonbreeding female group members are atrophic and lack corpora lutea (Swanson & Lockley 1978).

The reproductive skew seen in caged families of Mongolian gerbils is unlikely to be a laboratory artefact. In natural circumstances, a gerbil burrow is often inhabited by a mix of adults, subadults and juveniles, including older siblings that remain in the parental burrow for their first winter (Fetisov & Moskovskiy 1948; Bannikov 1954; Leont'ev 1954, 1962). Frequently, in the field (Gromov 1981; Agren 1989), as in seminatural conditions (Agren 1976), only one female in a group sharing a burrow is reproductively active, so sexual maturation of young female gerbils that remain with their parents can be much delayed.

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Reproductive skew like that seen in gerbils is frequently interpreted as resulting from either reproductive suppression of subordinate females by more dominant individuals of the same sex (e.g. Batzli et al. 1977; Wasser & Barash 1983; Gubernick & Nordby 1992; Bennett et al. 1994; Reeve et al. 1998) or incest avoidance mechanisms (e.g. Hoogland 1982; Blouin & Blouin 1988; Wolff 1992; Burda 1995; Pusey & Wolf 1996). Consistent with the first of these interpretations, Payman & Swanson (1980) and Swanson & Lockley (1978) attributed failure of many young female gerbils to achieve reproductive maturity when maintained in their natal families to suppressive effects of an older, actively breeding female. Swanson & Lockley (1978) found that if the mother of a family group of gerbils was removed, her daughters showed rapid development of their scent glands, and Payman & Swanson (1980) report that after a mother died her daughters were significantly more likely to reproduce than when she was present. However, in Payman & Swanson's (1980) study, only those young females whose dams were rearing second litters failed to develop adult secondary sexual characteristics. It therefore remains possible that presence of a second litter, rather than of a dam, was responsible for the reproductive suppression of young females observed in Swanson's studies (Swanson 1983).

Results of laboratory studies (Agren 1984) also suggest that, as in some other rodent species (Haigh 1983; Schadler 1990; Terman 1992), prolonged exposure of gerbil family members to one another, rather than actual consanguinity, is both necessary and sufficient to produce reproductive suppression in females. Consequently, reproductive skew occurs in 'families' consisting of foster parents and young as well as in natural families (Swanson 1983). Dependence of reproductive delay in female gerbils on familiarity, rather than on consanguinity, is fortunate because it permits random assignment of subjects to conditions as well as extensive experimental manipulation of family structure to determine the causes of reproductive failure within family groups of gerbils.

Families and other social groups are complex, dynamic systems in which there are potential conflicts of interest among all members. Consequently, one might expect to see considerable complexity in the ways in which group members of the same and opposite sex influence one another's reproductive activities (e.g. Vehrencamp 1983; Haigh 1987; Emlen 1991; Keller & Reeve 1994; Clutton-Brock 1998).

Here, we report results of a single experiment in which we examined effects of group composition on rate of reproductive maturation in female members of 240 artificially constituted family groups of Mongolian gerbils. We had hoped that by looking at the simultaneous effects of several different variables on rates of female sexual maturation we would be able to identify one or two major determinants of reproductive skew in female gerbils. However, results of the experiment described below provided evidence of several effects on female reproductive maturation, as well as of interactions among them.

The complexity of the results led us to present the single experiment that we conducted as three separate studies. Comparisons of data across these three studies are statistically legitimate in that all were run concurrently, and subjects were randomly assigned amongst them.

STUDY 1: EFFECTS OF SISTERS ON ONE ANOTHER'S RATES OF REPRODUCTION

If sisters inhibit one another's rates of sexual maturation (e.g. Getz et al. 1983; Drickamer 1986; Haigh 1987; Gudermuth et al. 1992), one might expect to find a correlation between the number of females in a litter and the frequency with which the reproductive activity of the female members of a litter is either blocked or delayed. In study 1, we determined the frequency and rate of sexual maturation in litters of one, two or three sisters raised by foster parents. By using foster litters as subjects, we were able to control both the size and sex composition of litters, factors that in gerbils, are known to affect parental responses to young (Clark & Galef 1990; Clark et al. 1991).

Methods

Subjects

Sixty litters of Mongolian gerbils and their parents participated in study 1. All were third-generation descendants of breeding stock acquired from Charles River Breeding Farms (Wilmington, Massachusetts, U.S.A.) and all were born and reared in the vivarium of the McMaster University Department of Psychology (Hamilton, Ontario, Canada).

The colony occupied 100–120 cages in a single temperature- and humidity-controlled colony room illuminated on a 12:12 h light:dark cycle. All subjects had ad libitum access to Purina Rodent Laboratory Chow 5001 and water throughout life.

Rearing conditions

Each breeding pair resided in a polycarbonate, shoe-box cage, measuring 30 × 15 × 18 cm. The cage was closed with a wire-rod lid and its floor was carpeted with a layer of wood-chip bedding. When a female became obviously pregnant (in her third week of gestation), she received 20–30 g of cotton batting with which to build a nest.

Procedure

On the day of birth of a litter, we removed its members and replaced them with a foster litter containing three or four males and three or four females that had been born within 24 h of the time of birth of the foster parents' own litter. Litters and their foster parents remained undisturbed (except for biweekly cage cleaning) until litters were 32 days old, when we removed all juvenile males and all but one (20 cages), two (20 cages) or three (20 cages) female pups from each cage.

To prevent any litter cannibalism, when a foster daughter became visibly pregnant in the third week of gestation, we removed her from the cage she shared with her foster parents and sisters, and established her in a separate cage. At the same time that we removed the pregnant young female from a cage, we determined for those cages containing more than one young female, whether any young female other than the one we were removing was pregnant. We also removed any litters born to foster mothers on the day of the litter's birth.

We determined: (1) the percentage of cages containing one, two or three foster daughters in which a young female gave birth during the 12 weeks following weaning on day 32 postpartum, and (2) the mean age at parturition of the first juvenile female to become pregnant in each cage in which a juvenile female reproduced. Limiting data analysis to only one measure of age at parturition per cage is a conservative approach assuring statistical independence of measurements.

Results and Discussion

There was a clear effect of number of sisters in a cage on the probability that one would reproduce by the time she was 116 days of age. The smaller the number of sisters in a cage the greater the probability that one of them would bear young (chi-square test, Yate's correction: χ^2_2=11.9, P<0.03; Fig. 1). This result is all the more striking given that, other things being equal, the probability that a cage would contain a young female that reproduced should have increased with the number of sisters in a cage.

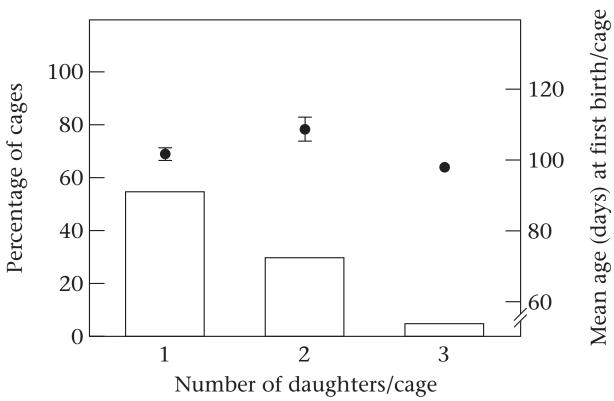

Figure 1. Left ordinate and histograms: percentage of cages in which one or more young females in study 1 became pregnant by 116 days of age; right ordinate and points: mean age at which the first young female in each of these cages became pregnant. Error bars=1 SEM.

The mean age at which the first foster daughter in each cage that contained two or three sisters reproduced varied marginally as a function of the number of sisters in a cage (Student's *t* test: t_{15}=2.02, P<0.06).

Whereas frequency of reproduction by daughters decreased as their numbers increased, reproduction by foster mothers was unaffected by the number of foster daughters she was rearing. Fifty-eight of 60 foster mothers continued to produce litters throughout the study, and the mean number of litters that they produced was not affected by the number of young females in their respective cages (ANOVA: $F_{2,57}$=1.16, NS).

Although the results of study 1 are consistent with the hypothesis that sisters inhibited one another's sexual maturation, other explanations of the data are possible. For example: (1) foster mothers may inhibit reproduction by young females in her presence, but the number of female young that a foster mother is rearing may determine the strength of the inhibitory signal she emits, (2) the number of females in a cage, independent of the females' reproductive status, may be an important factor in producing reproductive suppression, or (3) exposure of foster fathers to young females may inhibit males' sexual response to females (Skryja 1978; Swanson 1983), and the strength of that inhibition may increase with the number of young females to which a foster father is exposed.

STUDY 2: FEMALES WITHOUT THEIR MOTHERS: EFFECTS OF FAMILIAR AND UNFAMILIAR FOSTER FATHERS

In study 2, we examined rates of maturation of female gerbils caged with their sisters and foster fathers, but without their foster mothers. In the absence of foster mothers, we could replace foster fathers with unfamiliar males to determine effects of familiarity of a foster father with the litter that he had reared on rates of impregnation. Furthermore, by comparing results of study 2, in which foster mothers were absent, with those of study 1, in which foster mothers were present, we could determine effects of foster mothers on their foster daughters' reproduction.

Methods

Subjects

One hundred and twenty litters and their foster parents as well as 60 additional fathers participated in the study.

Procedure

In the present study, on day 32 postpartum, we removed all mothers, all sons and varying numbers of daughters from the 60 litters randomly assigned to the control condition, leaving 20 foster fathers with one, 20 foster fathers with two, and 20 foster fathers with three foster daughters that they had helped to rear.

We treated subjects assigned to the experimental condition as we treated those assigned to the control condition except that, on day 32 postpartum, we also replaced each foster father with another male. These 'replacement foster fathers' had served as foster fathers to litters born on the same day as the litters reared by the foster fathers that they replaced. Like foster fathers assigned to the control condition, replacement foster fathers assigned to the experimental condition were caged with either one (20 replacement males), two (20 replacement males) or three (20 replacement males) 32-day-old sisters.

As in study 1, when a female was in her third week of gestation, we removed her to a separate cage to prevent any litter cannibalism.

Results and Discussion

Effects of presence of a replacement foster father on reproduction

Young females assigned to the control condition (those that shared a cage with the foster father that had reared them) were far less likely to give birth than foster females assigned to the experimental condition (those that shared a cage with a replacement foster father) (chi-square test, Yate's correction: χ^2_1=20.87, P<0.0001; Fig. 2). However, young females in control and experimental conditions that gave birth did so at the same age independent of group assignment (ANOVA: $F_{1,71}$=1.59, NS). Either familiar foster fathers were less adequate releasers of sexual behaviour in young females than were replacement foster fathers (Carter et al. 1980; Hofman & Getz 1988), or foster fathers were less willing to copulate with the females in their cage than were replacement foster fathers that had not participated in the rearing of the females in their respective cages (Surbey 1990; Terman 1992).

Effects of presence of a foster mother on reproduction

In study 1 (in which we left sisters with both their foster father and a reproductively active foster mother; Fig. 1) foster daughters bred in 18 of 60 cages (30%). In the control group of the present study (in which we left sisters with their foster fathers and no reproductively active female was present), females bred in 26 of 60 cages

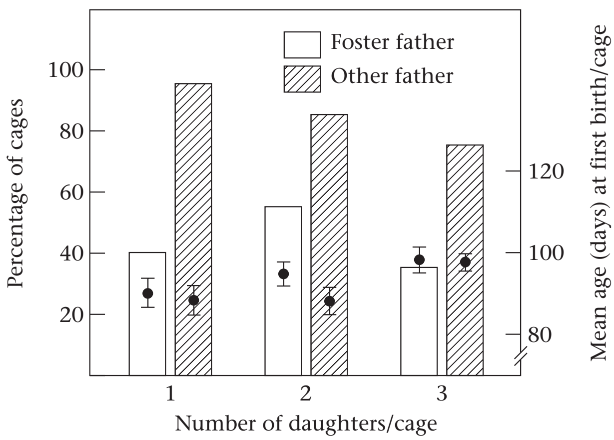

Figure 2. Left ordinate and histograms: percentage of cages in which one or more females in study 2 became pregnant by 116 days of age; right ordinate and points: mean age at which the first female in each of these cages became pregnant. Open histograms and the points they contain refer to the control group; hatched bars and the points they contain refer to the experimental group. Error bars=1 SEM.

(43%). A chi-square test comparing frequency of impregnation of young females in study 1 and the control group in study 2 revealed no significant effect of foster mothers' presence on foster daughters probability of reproduction (Yate's correction: χ^2_1=1.78, NS). Even the less conservative approach of examining the number of young females in cages containing one, two or three sisters that became pregnant in the two studies revealed no effect of mother's presence on frequency of pregnancy in foster daughters (Yate's correction: χ^2_2=4.01, NS). However, as would be expected on the hypothesis that exposure to adult females retards reproductive development in younger females, the mean age at which the first young female in each cage containing one or two daughters became pregnant was significantly higher in study 1 than in study 2 ($F_{1,32}$=19.75, P<0.001). (We excluded cages with three daughters from the analysis because only one such female reproduced in study 1 and it is not possible to conduct an ANOVA when a cell has only a single data point.)

Comparison of the magnitude of effects on reproductive activity of young females of removal of their mother (compare Fig. 1 and open histograms in Fig. 2) with effects either of male familiarity (Fig. 2) or numbers of sisters (Fig. 1), suggests that the effects of presence of an older, reproductively active female on reproduction by younger females may depend on the number of sisters present in a litter. For example, in study 1, three daughters housed with a dam bred in only 5% of cages, whereas three daughters housed without a dam bred in 38% of cages (Fisher's exact test: P<0.05). In contrast, in study 2, 40% of single daughters caged with their dam bred, and single daughters housed without a dam bred in 44% of cages (Fisher's exact test: P=1.0).

Effects of number of sisters on reproduction

In contrast to the outcome of study 1, in which both foster parents remained with litters after day 32 postpartum, in study 2, we found no effect of number of sisters in a cage on the probability that sisters living either with their foster fathers (Yate's correction: χ^2_2=1.77, NS; Fig. 2) or a replacement foster male (Yate's correction: χ^2_2=3.10, NS; Fig. 2) would be impregnated by the male in their cage.

In study 2, as in study 1, the number of sisters in a cage also failed to affect the age at which the first female in each cage to become pregnant gave birth when daughters were living with their foster fathers (ANOVA: $F_{2,23}$=1.42, NS; Fig. 2). However, the number of sisters in a cage did have a marginal effect on the age at which the first female in each cage to become pregnant gave birth when daughters lived with replacement foster fathers ($F_{2,48}$=3.04, P<0.06; Fig. 2).

The significant effect of number of sisters present on the frequency with which they became pregnant in study 1, but not in the control group of study 2, suggests an interaction between adult females and the young they are rearing affecting the probability of reproduction by the young. Expression of the mutual inhibition by sisters of one another's reproductive development observed in study 1 appears to be mediated in some way by the presence of a reproductively active adult female.

STUDY 3: EFFECTS OF REARING YOUNG ON ADULT MALES

The results of study 2 indicated that sexual maturation of females is slowed if they are exposed after weaning only to the male that participated in their rearing (Fullerton & Crowley 1971; Vandenbergh 1972, 1973). As discussed above, possibly: (1) exposure of a male to maturing females reduces his readiness to mate with the females to which he has been exposed (Carter et al. 1980; Zeigler et al. 1987; Widowski et al. 1990; Burda 1995), or (2) females are reluctant (or unable) to mate with a male who reared them (McGuire & Getz 1990). Other effects of rearing females on a male's reproductive potential are also possible.

In the present study, we determined whether participation in the rearing of young females affected a male's subsequent ability to impregnate young females other than those he helped to rear.

Methods

Subjects

Sixty adult male Mongolian gerbils and 120 32-day-old female gerbils from 60 litters served as subjects. The males had not fathered or had any contact with young gerbils for at least 30 days before we paired them with the female subjects.

Procedure

The procedures used were identical to those used with the experimental group in study 2 (i.e. when a litter reached 32 days of age, we removed the dam, father and sufficient offspring, so that each of 20 cages contained one, two, or three young females). However, in the present study, instead of replacing each litter's foster

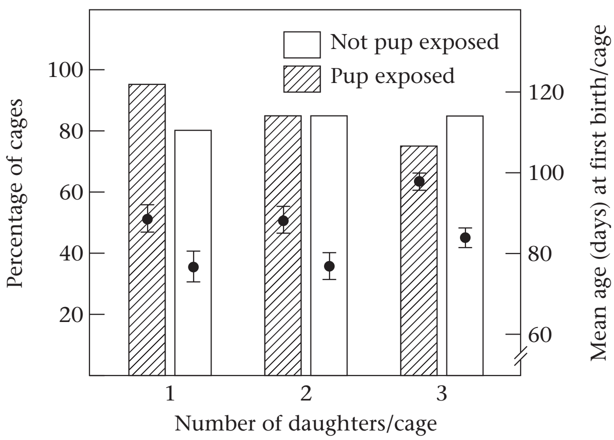

Figure 3. Left ordinate and histograms: percentage of cages in which one or more young females in study 3 became pregnant by 116 days of age; right ordinate and points: mean age at which the first female in each of these cages became pregnant. Open histograms and the points they contain refer to exposed males in the present study; hatched histograms and the points they contain are data from the experimental group in study 2, and are presented for purposes of comparison. Error bars=1 SEM.

father with a male that had, for the preceding 32 days, participated in rearing a litter, we replaced each foster father with a male that had not had contact with infant or juvenile gerbils for at least 30 days (a not-exposed male).

As in previous studies, we: (1) removed juvenile pregnant females late in gestation, and (2) determined both the number of cages in which a female gave birth and the mean age at parturition of the first juvenile female in each cage in which a juvenile female gave birth.

Results and Discussion

Effects of previous experience with litters on males' reproduction

Comparison of the results of the present study with data from young females interacting with replacement foster fathers in the experimental group of study 2 revealed no effect of males' recent previous contact with a litter on the probability that he would impregnate one or more of the unfamiliar young females with which he was placed (chi-square test, Yate's correction: χ^2_1=0.25, NS; Fig. 3). However, there was a highly significant effect of previous exposure of males to litters on the latency with which males impregnated young females (ANOVA: $F_{1,96}$=18.97, P<0.001; Fig. 3). Males that had recently participated in fathering and rearing a litter were either less sexually active or less attractive to young females than males lacking such experience.

Effects of number of daughters

As in study 2, in the absence of a reproductively active older female, the number of sisters in a litter had no effect on the probability that one female in a cage would give birth (chi-square test, Yate's correction: χ^2_2=3.14, NS; Fig. 3), but did affect age at delivery of the first female in a cage to become pregnant (ANOVA: $F_{2,91}$=4.20, P<0.02; Fig. 3), indicating an inhibitory effect of sisters on one another's rates of sexual maturation.

Further evidence of such inhibition was provided by the finding in the present study that unfamiliar replacement males fertilized 16 of 20 (80%) single females, but only 26 of 40 (65%) females housed in cages containing two sisters and 25 of 60 females (42%) maintained in cages containing three sisters (chi-square test, Yate's correction: χ^2_2=11.00, P<0.004).

GENERAL DISCUSSION

Taken together the results of the present experiment suggest that familial control of reproductive activity in young female gerbils is complex even in artificially simplified situations such as those studied here, where influence of brothers on their sisters reproductive development was excluded. Results of study 1 indicate that young sisters can inhibit one another's reproductive development, although the results of studies 2 and 3 suggest that expression of this inhibition is affected in some way by presence of an older, reproductively active female.

Results of study 2 show either that: (1) sexual incompatibility develops between male gerbils and females that they help to rear, or (2) female gerbils need to be exposed to an unfamiliar male if their reproductive development is to proceed to completion.

Finally, study 3 provides what we believe is a unique finding, that a male's participation in the rearing of young females increases his latency to engage in sexual behaviour, presumably by rendering him either less sexually active or less attractive to females.

The results of the present series of studies are consistent with two general lines of interpretation. First, and as is generally assumed, female gerbils appear to suppress one another's reproductive activity, with the intensity of such suppression varying markedly with social context.

Second, the data are consistent with the hypothesis that reproductive delay or failure in female gerbils can result from absence of stimulation by an unfamiliar male (Widowski et al. 1990). Replacement of a foster father with an unfamiliar male had a major effect on the reproductive activity of young females (see French 1997 for similar findings in primates).

As we have indicated in discussions of the individual studies, most of the findings in the present experiment are open to more than one interpretation. We are currently engaged in experiments to determine the conditions under which: (1) recent experience rearing female juveniles interferes with a male gerbil's probability of securing copulations, (2) female gerbils reared together inhibit one another's reproductive maturation, (3) exposure to an unfamiliar male accelerates female gerbils' reproductive development, and (4) familiarity of males and young females induces sexual incompatibility. Only when the processes supporting such social influences on the reproductive maturation of female gerbils have been examined in detail will it be possible to begin to understand the relationship between such laboratory phenomena and the reproductive life histories of Mongolian gerbils living in natural habitat.

Acknowledgments

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