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Effects of Siblings on Reproductive Maturation and Infanticidal Behavior in Cooperatively Breeding Mongolian Gerbils

ABSTRACT: *Mongolian gerbils living with their natal families undergo delayed reproductive maturation while helping to rear their younger siblings, whereas those housed away from their natal families may mature earlier but often respond aggressively to unfamiliar pups. We tested whether cohabitation with pups contributes to reproductive suppression and inhibition of infanticidal behavior, using young males and females housed with (1) their parents and younger siblings (pups), (2) parents without pups, (3) mixed-sex littermate groups, or (4) mixed-sex groups of unrelated peers. Maturation in males was inhibited by cohabitation with the parents, while maturation in females was further suppressed in the presence of pups. Males in all housing conditions showed little aggression towards unfamiliar pups, whereas females were usually infanticidal unless housed with pups. Aggression toward pups was especially pronounced in females that were pregnant or undergoing ovulatory cycles. Thus, cohabitation with younger siblings may intensify reproductive suppression and inhibit infanticidal behavior in female gerbils, whereas male gerbils exhibit parentally induced reproductive suppression and low rates of infanticide even in the absence of younger siblings.* © 2008 Wiley Periodicals, Inc. Dev Psychobiol

Keywords: *Mongolian gerbil; reproductive suppression; infanticide; aggression; alloparental behavior; cooperative breeding; progesterone*

INTRODUCTION

Cooperative breeders live in groups in which behaviorally subordinate individuals often fail to reproduce and instead provide care for the offspring of the dominant, breeding male and female. In many species, these groups comprise families, in which the nonbreeding subordinates are the offspring of the dominant, breeding pair and help to rear their own younger siblings. Reproductive suppression in these subordinates appears to depend largely upon

inhibition imposed by, or in response to, the same-sex breeder/parent. In some species, however, siblings, in addition to the parents, may play a role in determining the occurrence or extent of reproductive suppression in subordinates. In common marmosets (*Callithrix jacchus*; Saltzman, Pick, Salper, Liedl, & Abbott, 2004; Saltzman, Schultz-Darken, & Abbott, 1997), cotton-top tamarins (*Saguinus oedipus*; Heistermann, Kleis, & Prove, 1989), and naked mole-rats (*Heterocephalus glaber*; Clarke & Faulkes, 1997; Margulis, Saltzman, & Abbott, 1995), for example, ovulatory activity in young adult females living with their natal families can be inhibited by agonistic interactions not only with the mother but also with sisters.

Interactions with siblings, especially younger siblings, may also play a key role in the development of alloparental behavior and may have long-term effects on an individual's responsiveness to infants. In prairie voles

(*Microtus ochrogaster*), for example, previous experience with younger siblings was shown to enhance alloparental responsiveness toward unfamiliar pups in juvenile and subadult males and females (Roberts, Miller, Taymans, & Carter, 1998; but see Lonstein & De Vries, 2001). In California mice (*Peromyscus californicus*), juvenile males and females showed enhanced alloparental responsiveness if they were housed with their parents and younger siblings, but not with their parents alone (Gubernick & Laskin, 1994). Few studies, however, have systematically investigated the effects of siblings on either alloparental responsiveness or reproductive inhibition in cooperative breeders.

Mongolian gerbils (*Meriones unguiculatus*) are cooperatively breeding, cricetid rodents in which cohabitation with siblings has been hypothesized to influence both reproductive suppression and responsiveness to pups. Under natural or seminatural conditions, groups may comprise a breeding pair, their pups, and several of their previous litters (Ågren, 1976; Ågren, Zhou, & Zhong, 1989: Roper & Polioudakis, 1977; Swanson & Lockley, 1978). Offspring of both sexes may remain with their parents for prolonged periods as nonbreeding alloparents. Sons living with their natal families have been reported to have smaller absolute and relative testicular and epididymal masses, as compared to their fathers, but no differences in fecal testosterone concentrations or extent of spermiogenesis (Scheibler, Weinandy, & Gattermann, 2006). Daughters living with their natal families, on the other hand, frequently show suppression or delay of reproductive maturation, as evidenced by atrophic uteri, small ovaries with no corpora lutea or large follicles, minimal development of the gonadal-steroid-dependent ventral scent gland, and failure to breed (Payman & Swanson, 1980; Saltzman, Ahmed, Fahimi, Wittwer, & Wegner, 2006; Swanson & Lockley, 1978).

The specific stimuli determining reproductive suppression in gerbils are not clear. Swanson and Lockley (1978) found that when mothers were removed from families, their daughters often exhibited rapid scent-gland development and sometimes began to breed. Payman and Swanson (1980), however, found that mothers inhibited scent-gland development in their daughters only if a subsequent litter of pups was also present. Similarly, French (1994) demonstrated that when daughters conceived while living with their natal families, they did so during periods when their mothers had extended interbirth intervals. Finally, Clark and Galef (2001) found that sisters inhibited reproductive development in one another, and that this effect was enhanced in the presence of a reproductively active older female. Thus, mothers, younger siblings (pups), and littermate sisters have all been implicated in suppressing reproductive function in

female gerbils, while the specific stimuli suppressing reproductive development in males have not been investigated.

Cohabitation with the natal family also inhibits aggressiveness toward pups in female Mongolian gerbils. Although females and males living with their natal families commonly engage in alloparental behavior (Ostermeyer & Elwood, 1984), most adult females housed apart from their natal families are infanticidal when tested with unrelated, unfamiliar pups, and behave maternally only during lactation and the final days of pregnancy (Elwood, 1977, 1980, 1981; Saltzman et al., 2006). In a recent study, most young adult females that were housed either singly or with another young female attacked unfamiliar, unrelated pups, whereas age-matched females that were housed with their parents and siblings never did so (Saltzman et al., 2006), even though all of the females had previously lived with pups (younger siblings). Thus, infanticide in family-housed females appears to be inhibited by cohabitation with the parents and/or by ongoing interactions with pups. Adult male gerbils may also behave aggressively toward unfamiliar, unrelated pups, but do so less consistently than adult females (Elwood, 1977, 1980).

In the present experiment we investigated the effects of younger siblings on both reproductive maturation and infanticidal behavior in male and female Mongolian gerbils. Specifically, we aimed, first, to test the hypothesis that females housed with their parents undergo reproductive suppression only if pups are present (Payman & Swanson, 1980; see also French, 1994), and to determine whether the presence of younger siblings also contributes to reproductive suppression in males. Second, we tested the hypothesis that inhibition of infanticidal behavior in females depends upon cohabitation with younger siblings, rather than simply with the parents (Saltzman et al., 2006), and investigated whether a similar effect occurs in males. To do so, we compared reproductive development and responses to unfamiliar, unrelated pups in young male and female gerbils that were housed with their parents and a littermate, either with or without pups. To control for effects of the parents, we also characterized reproductive development and infanticidal behavior in males and females that were housed in small, mixed-sex groups of either littermates or unrelated, age-matched conspecifics.

Several hormones are known to facilitate (e.g., estrogen, prolactin, oxytocin) or inhibit (e.g., testosterone) parental responsiveness in rodents (Numan & Insel, 2003). We chose to focus on progesterone, for several reasons. First, anecdotal observations in our laboratory suggest that pregnancy may increase infanticidal behavior in female gerbils (unpublished data; see also Elwood, 1977, 1981), similar to several other cooperatively breeding mammals (e.g., Clutton-Brock et al., 1998;

Saltzman, 2003). Second, progesterone and progesterone receptors inhibit paternal behavior and increase infanticidal behavior in male laboratory mice (Schneider et al., 2003; but see Nephew, Lovelock, & Bridges, 2008), and plasma progesterone concentrations correlate negatively with paternal behavior in California mice, a species that, like Mongolian gerbils, spontaneously engages in high levels of paternal behavior (Trainor, Bird, Alday, Schlinger, & Marler, 2003) Therefore, we characterized plasma progesterone concentrations, in addition to body mass, reproductive organ masses, ovulatory status, and development of the gonadal-hormone-dependent ventral scent gland. We predicted that both reproductive development and infanticidal behavior would be inhibited in females living with their parents, compared to those living away from their parents, and that these effects would be more pronounced in the presence rather than in the absence of younger siblings. Because male Mongolian gerbils undergo less intense reproductive suppression than females (Scheibler et al., 2006; Swanson & Lockley, 1978) and exhibit lower rates of infanticide (Elwood, 1977, 1980), we further predicted that the effects of parents and younger siblings on reproductive development and infanticidal behavior would be less pronounced in males than in females.

METHODS

Animals

We used F1 and F2 descendants of Mongolian gerbils purchased from Harlan (Indianapolis, IN; see Brain, 1999; Saltzman et al., 2006 for details of the Harlan colony). Animals were housed in clear polycarbonate cages (48 cm × 27 cm × 20 cm) containing corn-cob bedding, paper towels for nesting material, and a tin can (13 cm long × 10 cm diameter) for enrichment. Food (Purina Rodent Chow 5001) and water were available ad lib, and supplements of carrots, oats, and sunflower seeds were each provided once per week. Lights were on from 0700 to 1900 hr, and room temperature and humidity were maintained at approximately 23°C and 30–70%, respectively.

Design

Each of 43 female and 43 male gerbils was assigned at weaning (approximately 21 days of age) to one of four housing conditions: Parents + Pups ($N = 9$ males + 9 females), Parents Only ($N = 11$ males + 11 females), Sibling Group ($N = 11$ males + 11 females) or Unrelated Group ($N = 12$ males + 12 females). For the Parents + Pups and Parents Only conditions, one male and one female littermate were randomly selected as subjects at weaning age, at which time all other siblings were permanently removed from the family. Because cohabitation with a pregnant female may inhibit infanticide in male gerbils, independently of cohabitation with pups (Clark, Liu, & Galef,

2001; Elwood 1977), we allowed the parents in both of these conditions to continue breeding, but for the Parents Only condition we removed pups from the family before the focal male and female could interact with them. In both of these conditions, the male and female subjects remained with their parents continuously, except that several days before the anticipated date of the dam's next parturition (based on an interbirth interval of 24–26 days (Marston & Chang, 1965) and on weekly body-mass measures of dams), the focal male and female were removed from the parents' cage at approximately 1500 hr and housed together in a separate cage until approximately 0900 hr the next morning. These overnight separations continued each night until parturition (4.4 ± 1.2 nights, mean ± SEM). In the Parents Only condition, all pups were permanently removed from the family before the focal male and female were reunited with their parents; thus, focal animals in this condition never saw or interacted with pups (except their own littermates). In the Parents + Pups condition, new litters were culled to four pups before the focal male and female were reunited with the family. Two sibling pairs in the Parents + Pups condition did not undergo any overnight separations from the parents. In the Sibling Group condition, two males and two females from a single litter were housed with their parents and siblings until approximately 21 days of age, when they were removed from the family cage and housed separately as a sibling group. In the Unrelated Group condition, male and female pups were housed with their parents and siblings until approximately 21 days of age, when they were removed from the family and placed in a group containing two unrelated, age-matched males and two unrelated, age-matched females. In all four conditions, therefore, subjects were housed, from the time of weaning, in groups containing two males and two females, which comprised four age-matched animals that were either littermates (Sibling Group) or unrelated to one another (Unrelated Group); or a brother, sister, and their parents (Parents Only, Parents + Pups). In the Parents + Pups condition, groups additionally contained up to eight younger siblings (up to four from each of two litters).

Each male and female subject underwent a single pup test (see below) at 79–90 days (11.3–12.9 weeks) of age and was sacrificed the following morning for blood-sample collection and reproductive-tract assessment (see below). We also characterized development of the ventral scent-gland (see below), which is dependent upon gonadal steroids (Wallace, Owen, & Thiessen, 1973; Yahr & Thiessen, 1975) and correlates with reproductive maturation (Payman & Swanson, 1980; Saltzman et al., 2006; Swanson & Lockley, 1978). Male and female gerbils have been reported to reach maturity at approximately 10–12 and 9–12 weeks, respectively (Marston & Chang, 1965). In the Sibling Group condition, we used only one randomly selected male and one randomly selected female from each sibling group as subjects. In the Unrelated Group condition we used all four unrelated animals from each group, and in the Parents + Pups and Parents Only conditions, we used both siblings (brother and sister) from each family. Cagemates underwent pup tests on the same day, with males tested first in half the groups within each condition, and females tested first in the other half. At least 30 min elapsed from reunion of the group,

following one animal's pup test, to the beginning of the next cagemate's test.

Behavioral Responses to Foster Pups

Each male and female subject underwent a pup test at 0900–1100 hr following the methods described by Saltzman et al. (2006). The focal animal remained in its home cage while its cagemates were removed and placed in an identical cage. After a 5-min habituation period, an unrelated, unfamiliar pup, 0–3 days old, was placed in the subject's cage, in a corner opposite the nest area, and the subject's behavior was scored on a laptop computer using the JWatcher event recorder program (Blumstein & Daniel, 2007). The test continued for a maximum of 10 min. At the end of the test period, the pup was removed and the subject's cagemates were returned to the cage. If the subject unambiguously attacked the pup (i.e., blood was observed on the pup or bedding) at any time, the test was terminated immediately and the pup was euthanized. All behavioral data were collected by a single observer.

Collection of Blood Samples and Assessment of Reproductive Tracts and Scent Glands

Gerbils were killed by CO_2 inhalation at 0900–0930 hr the morning after undergoing a pup test, and blood was collected by cardiac puncture into a heparinized syringe. We elected to euthanize gerbils 24 hr after they underwent pup tests, rather than immediately following tests, so that both/all subject animals from each family/group could be euthanized at the same time, and so that hormone levels would not be acutely affected by the testing procedures. Blood samples were collected within 3 min from initial disturbance to the animal and within 2 min from initial exposure to CO_2. Blood was immediately placed on ice and subsequently centrifuged at 2,600 rpm for 10 min at 4°C. The plasma fraction was aspirated and stored at −20°C until assayed.

Immediately following blood collection, animals were weighed to the nearest gram and their scent glands were measured and assessed using a 4-point scale as follows: 0—scent gland not visible; 1—pale yellow or pale orange coloration without distinct borders; 2—yellow or orange coloration with distinct borders; 3—brown coloration with distinct borders (Saltzman et al., 2006). We additionally measured the length and greatest width of each scent gland that was rated 2 or 3 and calculated scent-gland area using the formula for area of an ellipse (length × width × pi).

Ovaries, uteri and testes were excised and cleaned of connective tissue, and their wet weights were determined to ±.0001 g. Ovaries were examined under a dissecting microscope, and the diameters of corpora lutea or of the largest follicles seen were recorded. Females were considered to be ovulatory if their ovaries contained one or more large follicles (≥1.0 mm) and/or corpora lutea, pregnant if corpora lutea and fetuses were observed, and anovulatory if the ovaries contained only small follicles (<1.0 mm) and no corpora lutea (Saltzman et al., 2006).

Progesterone Assay

Plasma progesterone concentrations were determined in duplicate aliquots by enzyme immunoassay (EIA) following extraction with petroleum ether, as previously described (Saltzman, Schultz-Darken, Scheffler, Wegner, & Abbott, 1994; Saltzman et al., 2006). The assay previously had been fully validated for use with gerbil plasma (Saltzman et al., 2006). Assay sensitivity at 90% binding was 4.1 ng/tube (.82 ng/ml), and intra- and interassay coefficients of variation of two plasma pools assayed in quadruplicate in each assay were 7.86% and 12.71% for a low-progesterone pool (81% binding) and 4.90% and 12.86% for a high-progesterone pool (53% binding), respectively.

Data Analysis

Age at sacrifice differed marginally among males ($F[3, 39] = 2.299$, $p = .092$) and significantly among females ($F[3, 39] = 6.751$, $p = .001$) in the four housing conditions. In both sexes, animals housed in groups of unrelated individuals were 2–4 days older at sacrifice, on average, than animals in the other three housing conditions (Tabs. 1 and 2). To control for these differences, we used age as a covariate in most analyses.

Five females (one housed with parents + pups, one in a sibling group, and three in unrelated groups) were pregnant at the time of sacrifice. Data from these females were omitted from analyses of body mass, uterine mass and ovarian mass. Body mass was analyzed separately for each sex by analysis of covariance (ANCOVA), using housing condition as a factor and age as a covariate. Uterine mass, ovarian mass, testicular mass, and scent-gland area were analyzed by ANCOVA using housing condition as a factor and age and body mass as covariates; for scent-gland area, we used testicular mass as an additional covariate. Plasma progesterone concentrations were analyzed separately for males and females using housing condition as a factor and using age and ovarian mass or testes mass as covariates. For females, we used ovulatory status (presence or absence of large follicles or corpora lutea in the ovaries at sacrifice) as an additional factor in analyses of organ masses and progesterone concentrations. Body mass, uterine mass, ovarian mass, progesterone concentration, and scent-gland area were log-transformed to increase normality and homoskedasticity. Analyses were initially performed without interaction terms; interactions were subsequently tested, and significant interactions were added to the model. Post hoc pairwise comparisons following significant main effects of housing condition were performed by the least significant difference (LSD) test.

To examine possible predictors of infanticidal behavior, we performed a logistic regression for each sex, with aggression in pup tests as the dependent variable and housing condition, age, plasma progesterone concentration, and, for males, testes mass as independent variables. Female reproductive status (ovulatory vs. anovulatory) was analyzed by chi-square tests. Unlike males, most females had poorly developed scent glands that could not be measured reliably; therefore, we analyzed only their scent-gland development scores, using Kruskal–Wallis tests. Kruskal–Wallis tests were performed using Systat v. 5 for the Macintosh (Chicago, IL), and ANCOVAs and LSD tests were

Table 1. Proportion of Female Gerbils That Attacked Pups in Pup Tests, and Age, Body Mass, Reproductive Measures, Plasma Progesterone Concentration, and Scent-Gland Development Score at Sacrifice of Females in the Parents + Pups, Parents Only, Sibling Group, and Unrelated Group Conditions

Housing Condition	Age (Days)[a]	# Attacked Pup/Total #	# Ovulatory, Not Preg./ Total #	# Pregnant/ Total #	# Anovulatory/ Total #	Body Mass[b,c] (g)	Uterine Mass[b,d] (g)	Total Ovarian Mass[b,e] (g)	Plasma Progest. (ng/ml)[f]	Scent-Gland Score[a]
Parents + Pups (N = 9)	$83.78 \pm .57$[g]	1/9 (11.1%)	0/9	1/9 (11.1%)	8/9 (88.9%)	43.15 (40.46, 46.03)	.052 (.040, .067)	.014 (.013, .016)	16.11 (10.72, 24.16)	$.4 \pm .2$
Parents only (N = 11)	$82.27 \pm .56$[g]	9/11 (81.8%)	2/11 (18.2%)	0/11	9/11 (81.8%)	46.99 (43.85, 50.35)	.086[i] (.067, .112)	.017[i] (.016, .019)	11.72[j] (7.80, 17.62)	$.9 \pm .4$
Sibling group (N = 11)	$82.45 \pm .67$[g]	8/11 (72.7%)	3/11 (27.3%)	1/11 (9.1%)	7/11 (63.6%)	45.71 (43.25, 48.31)	.071[i] (.057, .088)	.015 (.014, .017)	22.91 (16.07, 32.66)	$1.4 \pm .4$
Unrelated group (N = 12)	$86.08 \pm .87$	5/12 (41.7%)	1/12 (8.3%)	3/12 (25.0%)	8/12 (66.7%)	48.98 (45.19, 53.09)	.100[i,j] (.071, .140)	.017[i] (.015, .019)	13.27[j] (8.34, 21.09)	$1.3 \pm .3$
p-value (main effect of housing condition)	.002	<.01	—	—	>.5 (NS)[h]	.013 (condition × age: $p = .014$)	.047 (condition × age: $p = .049$)	.048	.040	.174 (NS)

[a]Mean ± SEM.
[b]Excludes five pregnant females.
[c]Back-transformed adjusted mean (lower, upper 95% confidence limit); evaluated at 83.68 days of age.
[d]Back-transformed adjusted mean (lower, upper 95% confidence limit); evaluated at 83.76 days of age and body mass = 44.99 g; excludes one outlier with unusually large uterus.
[e]Back-transformed adjusted mean (lower, upper 95% confidence limit); evaluated at 83.68 days of age and body mass = 44.85 g.
[f]Back-transformed adjusted mean (lower, upper 95% confidence limit); evaluated at 83.70 days of age and ovarian mass = .015 g.
[g]$p < .05$ compared to unrelated group (least significant difference test).
[h]From chi-square test comparing proportion of ovulatory (including both pregnant and nonpregnant) versus anovulatory females among housing conditions.
[i]$p < .05$ compared to Parents + Pups (least significant difference test).
[j]$p < .05$ compared to Sibling Group (least significant difference test).

Table 2.   Proportion of Male Gerbils That Attacked Pups in Pup Tests, and Age, Body Mass, Combined Testes Mass, Plasma Progesterone Concentration, and Scent-Gland Area at Sacrifice of Males in the Parents + Pups, Parents Only, Sibling Group, and Unrelated Group Conditions

Housing Condition	Age (Days)[a]	# Attacked Pup/Total #	Body Mass (g)[b]	Total Testes Mass (g)[c]	Plasma Progesterone (ng/ml)[d]	Scent-Gland Area (mm²)[e]
Parents + Pups (N = 9)	83.78 ± .57	0/9	51.29 (48.31, 54.58)[f]	.914 (.863, .966)	5.94 (4.34, 8.17)	2.985 (2.594, 3.443)
Parents only (N = 11)	82.27 ± .56	3/11 (27.3%)	51.88 (49.09, 54.83)[f]	.847 (.805, .893)[f,g]	7.82 (5.46, 11.19)	3.304 (2.871, 3.811)
Sibling group (N = 11)	82.45 ± .67	2/11 (18.2%)	54.20 (51.29, 57.28)	.914 (.869, .962)	6.05 (4.60, 7.94)	2.999 (2.642, 3.404)
Unrelated group (N = 12)	84.58 ± .98	0/12	57.15 (54.20, 60.40)	.959 (.912, 1.012)	13.52 (8.77, 20.85)	3.020 (2.624, 3.467)
p-value (main effect of housing condition)	.092 (NS)	.636 (NS)	.036	.021	.239 (NS) (condition × testes mass: .033)	.697 (NS)

[a]Mean ± SEM.
[b]Back-transformed adjusted mean (lower, upper 95% confidence limit); evaluated at 83.3 days of age.
[c]Back-transformed adjusted mean (lower, upper 95% confidence limits); evaluated at 83.3 days of age and body mass = 53.79 g.
[d]Back-transformed adjusted mean (lower, upper 95% confidence limits); evaluated at 83.3 days of age and testes mass = .909 g.
[e]Back-transformed adjusted mean (lower, upper 95% confidence limits); evaluated at 83.3 days of age, body mass = 53.79 g, and testes mass = .909 g.
[f]$p < .05$ compared to Unrelated Group condition (LSD tests).
[g]$p < .05$ compared to Sibling Group condition (LSD tests).

performed using SAS v. 8 PROC MIXED (SAS Institute, Cary, NC). All results were assessed using a critical p value of .05 (two-tailed).

RESULTS

Females

Body Mass, Reproductive Maturation, and Scent-Gland Development. ANCOVA revealed that body mass of nonpregnant female gerbils at the time of sacrifice was significantly affected by an interaction between housing condition and age ($F[3, 30] = 4.202$, $p = .014$) as well as by a main effect of housing condition ($F[3, 30] = 4.258$, $p = .013$). Within the narrow range of ages at sacrifice, body mass tended to increase sharply with age in females housed with only their parents but not in the other housing conditions.

Only 11 of the 43 females ovulated prior to sacrifice ("ovulatory females"), as evidenced by corpora lutea in their ovaries, and five of these females had visible fetuses (see Tab. 1). In the remaining 32 females, only small follicles (<1.0 mm) and no corpora lutea were visible, indicative of anovulation. The proportion of ovulatory females did not differ significantly among the four housing conditions (chi-square $= 2.356$, $df = 3$, $p > .5$).

Uterine mass in nonpregnant females was significantly affected by an interaction between housing condition and age ($F[3, 27] = 2.977$, $p = .049$) as well as by main effects of housing condition ($F[3, 27] = 3.015$, $p = .047$), body mass ($F[1, 27] = 12.114$, $p = .002$), and ovulatory status (i.e., presence of corpora lutea; $F[1, 27] = 18.691$, $p < .001$) but not age ($F[1, 27] = .015$, $p = .902$). Uterine mass tended to increase with age among females housed with only their parents or in sibling groups, but not among females housed with their parents and pups or in unrelated groups (Fig. 1). Overall, uterine mass was significantly lower in females housed with their parents and pups than in females housed with their parents only ($p = .004$, LSD test), in sibling groups ($p = .041$), or in unrelated groups ($p = .001$), and was lower in sibling groups than in unrelated groups ($p = .049$).

Similarly, total ovarian mass in nonpregnant females varied with housing condition ($F[3, 31] = 2.946$, $p = .048$), body mass ($F[1, 31] = 45.165$, $p < .001$), and ovulatory status ($F[1, 31] = 57.298$, $p < .001$), but not with age ($F[1, 31] = .019$, $p = .891$). Females housed with their parents and pups had significantly smaller ovaries than females housed with only their parents ($p = .016$, LSD test) or in unrelated groups ($p = .044$; Fig. 2).

When all females, regardless of ovulatory or pregnancy status, were analyzed together, plasma progesterone concentrations differed significantly across the four
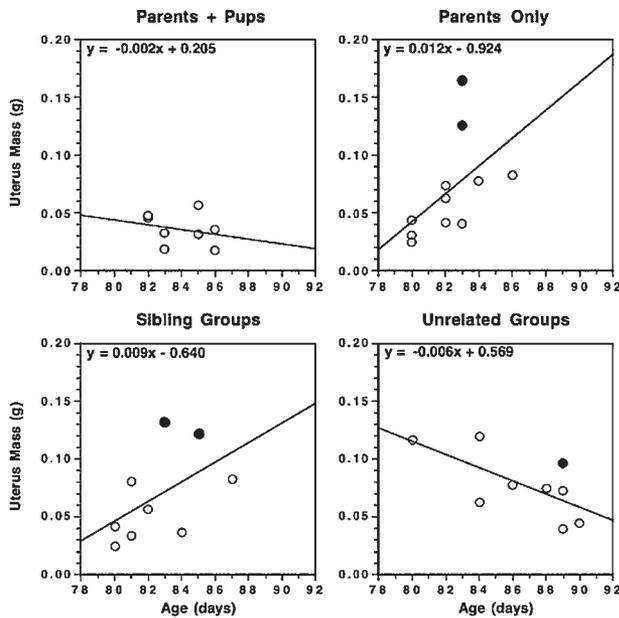
FIGURE 1 Uterine mass as a function of age among nonpregnant female gerbils in each of the four housing conditions. Data from one female with an unusually large uterus (.28 g) in a sibling group are not shown. White circles—anovulatory females (no large follicles or corpora lutea in ovaries); black circles—females with corpora lutea but no visible fetuses. Condition × age interaction: $p = .049$; main effect of condition: $p = .047$.
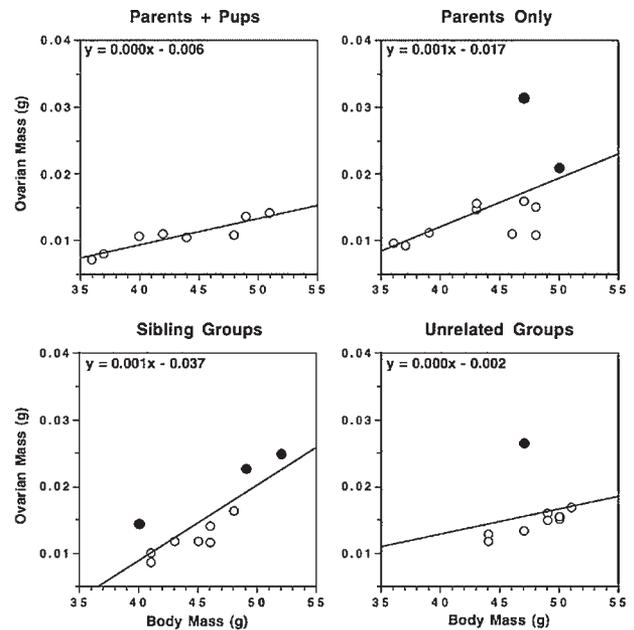

FIGURE 2 Total ovarian mass as a function of body mass among nonpregnant female gerbils in each of the four housing conditions. White circles—anovulatory females (no large follicles or corpora lutea in ovaries); black circles—females with corpora lutea but no visible fetuses. Main effect of condition: $p = .048$; main effect of body mass: $p < .001$.

housing conditions ($F[3, 36] = 3.064$, $p = .040$) and varied with ovarian mass ($F[1, 36] = 32.321$, $p < .001$). Females housed in sibling groups had higher progesterone levels than those housed either with their parents alone ($p = .007$, LSD test) or in unrelated groups ($p = .046$; see Tab. 1). Notably, the significant positive relationship between ovarian mass and plasma progesterone levels was evident even when anovulatory females were analyzed separately ($F[1, 26] = 14.983$, $p = .001$). Progesterone concentrations did not differ reliably with age ($F[1, 36] = .048$, $p = .828$) or between females that did and did not have corpora lutea in their ovaries ($F[1, 36] = 2.340$, $p = .135$), presumably because of the strong relationship between presence of corpora lutea and ovarian mass. When we repeated the analysis with ovarian mass excluded, progesterone concentrations were significantly higher in females with than in those without corpora lutea ($F[1, 37] = 67.954$, $p < .001$).

Only 25 of the 43 female gerbils (58.1%) showed any development of the ventral scent gland at the time of sacrifice, and only 12 of these (27.9% of all females) had scent glands that were moderately or well developed (development score = 2 or 3). Scent-gland development scores did not differ among females in the four housing conditions (Kruskal–Wallis $H = 4.973$, $p = .174$; Tab. 1). As expected, however, scent glands were more developed

in ovulatory than anovulatory females (Mann–Whitney $U = 52.000$, $N = 11.32$, $p < .001$).

Responses to Pups. Twenty-three of the 43 female gerbils (53.5%) attacked unfamiliar pups. The remaining 20 females sniffed, handled, and usually licked the pups; however, these animals were not highly maternal: only one retrieved a pup, and only two crouched over pups in a nursing posture.

Logistic regression revealed that aggression by females toward unfamiliar pups was significantly predicted by housing condition (Wald = 8.726, $df = 3$, $p = .033$) and plasma progesterone concentration (Wald = 6.202, $df = 1$, $p = .013$) but not age (Wald = .479, $df = 1$, $p = .489$). Only one of nine females housed with their parents plus pups attacked an unfamiliar pup, whereas nine of 11 females housed with only their parents ($p = .006$ compared to Parents + Pups), eight of 11 females in sibling groups ($p = .044$ compared to Parents + Pups), and five of 12 females in unrelated groups did so ($p = .575$ compared to Parents + Pups; Tab. 1). Plasma progesterone levels were higher in females that attacked pups than in those that did not (anti-log of mean [upper, lower 95% confidence limits]: 21.39 [25.71, 17.80] vs. 8.13 [9.67, 6.83] ng/ml, respectively). In a separate analysis, ovulatory

females across all four housing conditions were more likely to attack pups than were anovulatory females (chi-square $= 4.768$, $df = 1$, $p < .05$). Ten of 11 ovulatory females (90.9%) attacked pups, compared to 13 of 32 anovulatory females (40.6%). The only ovulatory female that did not attack a pup gave birth within 24 hr after her pup test, and in the Parents + Pups condition, the only female that ovulated was also the only one that attacked a pup.

Males

Body Mass, Reproductive Status and Scent-Gland Development. Body mass at the time of sacrifice differed among males in the four housing conditions ($F[3, 38] = 3.140$, $p = .036$): males housed in groups of unrelated peers were significantly heavier than those housed with their parents, either with pups ($p = .010$, LSD test) or without pups ($p = .019$; see Tab. 2). Body mass was not reliably predicted by age at sacrifice ($F[1, 38] < .001$, $p = .986$).

Total testes mass was significantly influenced by housing conditions ($F[3, 37] = 3.640$, $p = .021$) and body mass ($F[1, 37] = 63.123$, $p < .001$) but not by age ($F[1, 37] = .001$, $p = .324$; Tab. 2). Males housed with their parents but not pups had smaller testes than males in either sibling groups ($p = .038$, LSD test) or unrelated groups ($p = .003$), and tended to have smaller testes than males housed with their parents plus pups ($p = .054$; Fig. 3). Testes mass did not differ significantly among males in the latter three conditions.

Plasma progesterone concentrations in male gerbils were significantly influenced by an interaction between housing condition and testes mass ($F[3, 34] = 3.260$, $p = .033$) and by a main effect of testes mass ($F[1, 34] = 10.798$, $p = .002$), but not by age ($F[1, 34] = .008$, $p = .931$). Males housed with parents plus pups, parents alone, or sibling groups showed increasing progesterone levels with increasing testes mass, whereas males housed in unrelated groups did not show a consistent relationship between these two variables (Fig. 4).

All males had well-developed scent glands with brown coloration. Scent-gland area was influenced by body mass ($F[1, 36] = 4.422$, $p = .043$) and, marginally, by testes mass ($F[1, 36] = 3.928$, $p = .055$) but not by housing conditions ($F[3, 36] = .482$, $p = .697$) or age ($F[1, 36] = .688$; $p = .412$).

Responses to Pups. Only 5 of 43 males attacked pups in pup tests, a significantly lower proportion than in females (chi-square $= 15.304$, $df = 1$, $p < .001$). The remaining males sniffed, handled, and in many cases licked pups, and 10 of these males crouched over pups in a nursing posture. Logistic regression indicated that aggression by
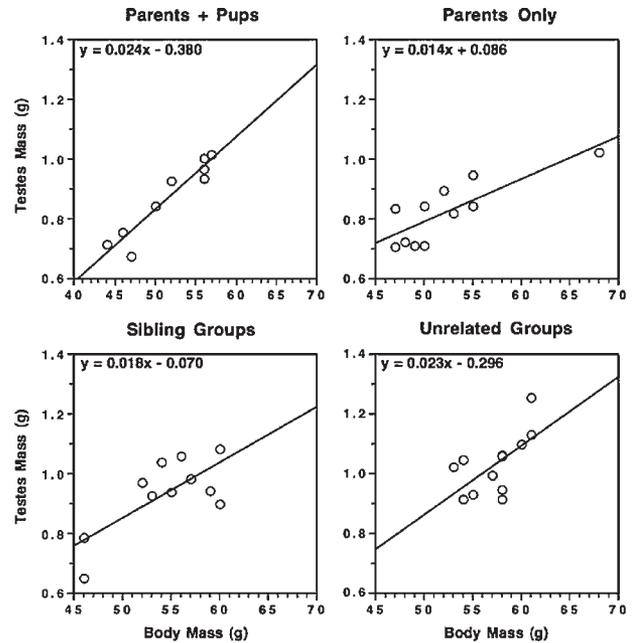

FIGURE 3 Total testes mass as a function of body mass among male gerbils in each of the four housing conditions. Main effect of condition: $p = .021$; main effect of body mass: $p < .001$.

males toward pups was not reliably predicted by housing condition (Wald $= 1.705$, $df = 3$, $p = .636$), age (Wald $= 1.156$, $df = 1$, $p = .282$), testes mass (Wald $= 2.490$, $df = 1$, $p = .115$), or plasma progesterone concentration (Wald $= 2.526$, $df = 1$, $p = .112$).
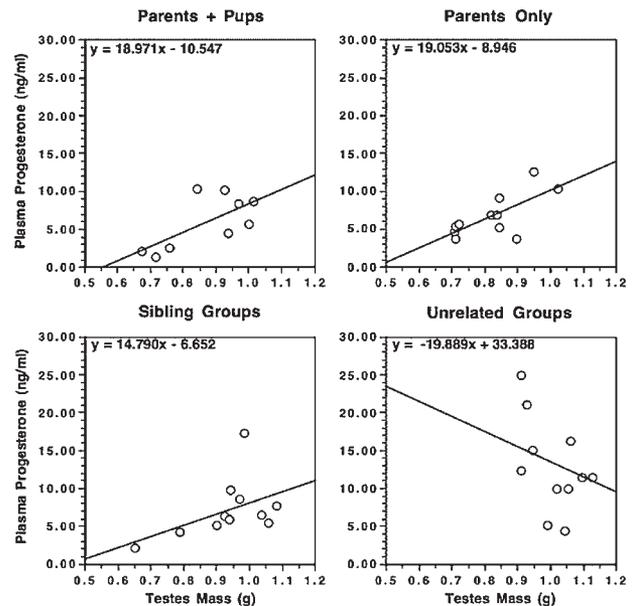

FIGURE 4 Plasma progesterone concentration as a function of total testes mass among male gerbils in each of the four housing conditions. Condition × testes mass interaction: $p = .033$; main effect of testes mass: $p = .002$.

DISCUSSION

Effects of Younger Siblings on Responses to Unfamiliar Pups

In this study we investigated the effects of siblings on infanticidal behavior and reproductive maturation in male and female Mongolian gerbils. Our results indicate that in young female gerbils, aggression toward pups is inhibited specifically by simultaneous cohabitation with younger siblings and parents, rather than by cohabitation with only the parents or other family members: aggression toward unfamiliar pups was rare among females housed with their parents and younger siblings, but common among those housed without pups, whether with their parents, littermates, or unrelated peers.

Our present findings do not indicate whether inhibition of infanticide requires ongoing cohabitation with pups, exposure to parents that are rearing pups, or simply prior experience with pups. In a previous study, however, we found that most young adult female gerbils housed alone or with a same-sex pairmate attacked pups in pup tests, even though all of the females had been housed with younger siblings previously (Saltzman et al., 2006). Thus, current cohabitation with younger siblings, but not previous experience with them, appears to strongly inhibit infanticidal behavior in young female gerbils. These results are comparable to findings in California mice, in which alloparental responsiveness of prepubertal males and females toward unfamiliar, unrelated pups was increased markedly by cohabitation with the parents and younger siblings, but not by cohabitation with only the parents and a single littermate (Gubernick & Laskin, 1994). In virgin Norway rats (*Rattus norvegicus*) and house mice (*Mus musculus*), cohabitation with the dam and her subsequent litter enhances future alloparental responsiveness, as compared to cohabitation with the dam in the absence of a subsequent litter (Lyons, 1993; Stern & Rogers, 1988). A somewhat different pattern has been reported in prairie voles, in which alloparental behavior of adult females toward unfamiliar pups was enhanced by cohabitation with the parents, whether or not younger siblings were present (Lonstein & De Vries, 2001). The ethological significance of these interspecific differences is unclear, but collectively these findings indicate that previous or ongoing exposure to pups may be an important source of variation in alloparental responsiveness of parentally inexperienced rodents.

Male gerbils in our experiment showed significantly lower rates of aggression toward unfamiliar pups than did females, and no effects of housing conditions on responses to pups. Similar sex differences in aggressiveness toward infants have been reported in previous studies of Mongolian gerbils (Elwood, 1977, 1980) as well as several other cooperative breeders, including prairie voles (Lonstein & De Vries, 1999; Roberts et al., 1998), dwarf hamsters (*Phodopus campbelli*; Vella, Evans, Ng, & Wynne-Edwards, 2005), common marmosets (Saltzman, Liedl, Salper, Pick, & Abbott, 2008), and meerkats (*Suricata suricatta*; Clutton-Brock et al., 1998). These findings may reflect sex differences in the intensity of reproductive competition in gerbils (Scheibler, Weinandy, & Gattermann, 2004) and other cooperative breeders, as females typically engage in more severe competition than males (Digby, 2000; Saltzman, 2003; Young & Clutton-Brock, 2006), resulting, perhaps, from sex differences in both the costs of reproduction and the certainty of parentage (Mumme, 1997).

Effects of Siblings on Reproductive Maturation

An unexpected finding in this study was that few females in any of the four housing conditions attained reproductive maturity (range: 11–36% of females per condition), as determined by the absence of large follicles or corpora lutea in the ovaries and confirmed by minimal development of the gonadal steroid-dependent ventral scent gland and low plasma progesterone concentrations in most females. In comparison, in a previous study of gerbils in the same age range, 25% of females housed with their parents and younger siblings, and 73% of individually housed or same-sex-paired females, were classified as ovulatory (Saltzman et al., 2006). The present results are difficult to interpret because we did not include singly or pair-housed control females in the present study; however, they suggest that all of the housing configurations used in this study may have inhibited female reproductive maturation to some extent.

Although most females in the present study did not attain reproductive maturity, plasma progesterone concentrations, uterine mass and ovarian mass differed significantly across housing conditions. Among non-pregnant females, those housed with their parents plus pups had smaller ovaries than those housed with their parents but not pups or in unrelated groups. Furthermore, nonpregnant females housed with their parents plus pups had reliably lower uterine masses than those housed with only their parents, and tended to have smaller uteri than those in sibling groups or groups of unrelated animals. These results are consistent with Payman and Swanson's (1980) finding that female Mongolian gerbils living with their mothers and female littermates exhibited reproductive suppression (as assessed on the basis of ventral scent-gland development) only if younger siblings were present in the family. The biological significance of the differences in uterine and ovarian mass in our study is not clear, however, in view of the absence of significant differences among housing conditions in the proportion of

females that ovulated or in scent-gland development. Moreover, although plasma progesterone concentrations differed reliably among housing conditions, females housed with their parents plus pups had relatively high progesterone levels that did not differ from those of females in the other conditions, and one of the nine females in the Parents + Pups condition became pregnant. Thus, our findings on uterine and ovarian masses must be interpreted cautiously.

Clark and Galef (2001, 2002) have suggested that reproductive maturation in young female gerbils can be delayed by cohabitation with any familiar individual, including littermates, parents, and unrelated adults (either gonadally intact or gonadectomized), and can be accelerated by exposure to an unfamiliar male. Therefore, we had anticipated that reproductive maturation would be delayed in females housed with littermates (sibling groups), as compared to those housed with unrelated peers (unrelated groups). We found inconsistent support for this prediction: females in sibling groups had significantly lower uterine masses but significantly higher plasma progesterone concentrations than those in unrelated groups. These findings suggest that if juvenile females first encounter unfamiliar conspecifics at a sufficiently early age (around the time of weaning, in this study), they may respond to these individuals as family members rather than as nonkin (see also Ågren, 1984). Alternatively, it is possible that maturation of young females in this study was influenced largely by housing density, rather than by the specific composition of the social groups (Hull, Chapin, & Kastaniotis, 1974).

Among males, physical and reproductive maturation were clearly affected by housing conditions: males housed with their parents (either with or without pups) had significantly lower body masses than males housed with unrelated peers, and males housed with only their parents had significantly smaller testes, when corrected for body mass, than males housed in either sibling groups or unrelated groups. These findings confirm a recent report that the family environment can inhibit reproductive maturation in male Mongolian gerbils (Scheibler et al., 2006) and suggest that cohabitation with one or both parents may be the critical determinant. Similar to females, maturation in males did not differ consistently between those housed with their littermates and those housed with unrelated peers. In contrast to females, however, we found no evidence that reproductive maturation in males was affected specifically by cohabitation with younger siblings, rather than or in addition to cohabitation with the parents. These sex differences in the social influences on reproductive development may be associated with sex differences in the patterning of aggression within Mongolian gerbil families. Females living with their natal families are most likely to be targeted for aggression by the group's breeding female (Scheibler et al., 2004); consequently, cohabitation with an actively breeding female (i.e., a female and her pups) may be a particularly salient stimulus eliciting reproductive restraint in females. Among young males, in contrast, reproductive maturation (e.g., elevated testosterone secretion, testicular growth, and the onset of spermiogenesis) appears to increase the risk of attack and expulsion by the father or by both parents (Scheibler et al., 2006); therefore, cohabitation with the parents, with or without younger siblings present, may be sufficient to elicit reproductive restraint in most young males.

Relationships Between Reproductive Maturation and Responses to Pups

Responses of male gerbils to an unfamiliar pup did not appear to be influenced by physical or reproductive maturation (body mass, testes mass, plasma progesterone concentrations, scent-gland area). Females' responses to pups, in contrast, were strongly associated with their reproductive state: females that were pregnant or undergoing ovulatory cycles were more than twice as likely to attack pups as were anovulatory, nonpregnant females (91% vs. 41%, respectively), and plasma progesterone concentrations significantly predicted females' responses to pups. These results contrast with our previous findings that agonistic responses to pups were not reliably associated with ovulatory activity or plasma progesterone levels in young female gerbils housed singly or in same-sex pairs (Saltzman et al., 2006). The most likely explanation for this disparity is that all females in the present study were housed with males; thus, ovulatory females were likely to be pregnant or pseudopregnant (Marston & Chang, 1965; Nishino & Totsukawa, 1996), whereas those in the previous experiment were not. Although only 5 of 11 ovulatory females in the present study had visible fetuses in their uteri at the time of sacrifice, the remaining six all had corpora lutea and therefore may have been pseudopregnant or in the very early stages of pregnancy. Mongolian gerbils have been shown to be highly infanticidal during pregnancy, until the last 6 days prepartum (Elwood, 1977). Interestingly, in the present study, the only female subject in the Parents + Pups condition that ovulated (and conceived) was also the only one to behave aggressively in a pup test, further reinforcing the link between ovulatory activity/pregnancy and infanticide, and indicating that the stimulatory effects of pregnancy on infanticidal behavior outweigh the inhibitory effects of cohabitation with pups.

In conclusion, the present findings suggest that reproductive maturation in male gerbils may be inhibited

specifically by cohabitation with the parents, whereas reproductive maturation in females may be inhibited by a broader range of social stimuli. Similar to a previous report (Payman & Swanson, 1980; see also French, 1994), reproductive suppression in females appears to have been intensified by the presence of pups, although this was a rather minor effect. Cohabitation with younger siblings in the presence of the parents additionally inhibited aggression towards unfamiliar pups in females, whereas activation of the hypothalamic–pituitary–ovarian axis was associated with enhanced aggression towards pups. Infanticidal behavior by males, in contrast, occurred infrequently and was not clearly affected by housing conditions or reproductive maturation. These sex differences in infanticidal behavior and in social regulation of reproductive development are consistent with sex differences in patterns of intrafamily aggression in Mongolian gerbils (Scheibler et al., 2004, 2006), and, more broadly, with widespread sex differences in the intensity of reproductive competition among cooperative breeders (Mumme, 1997).

Similar to Mongolian gerbils, reproductively active females in numerous other cooperatively breeding species (e.g., insects (Eggert & Müller, 2000; Keeping, 1992; Ratnieks & Visscher, 1989), birds (Mumme, Koenig, & Pitelka, 1983; Vehrencamp, 1977), carnivores (Clutton-Brock et al., 1998; Corbett, 1988; Packer & Pusey, 1984; Rasa, 1987), and primates (Saltzman et al., 2008)) may frequently behave aggressively toward other females' offspring, suggesting that infanticide may be a common mechanism of intrasexual reproductive competition in female cooperative breeders. Results of the present study indicate that such aggressiveness towards infants may be facilitated by the onset of reproductive activity, especially pregnancy or pseudopregnancy. Finally, our findings suggest that such competition may be triggered in Mongolian gerbils when a breeding female experiences reproductive failure, as the resulting absence of pups in the family may elicit a shift in her daughters from reproductive inhibition to reproductive activation, and from alloparental to infanticidal behavior. Thus, for nonbreeding females, but not males, in cooperative societies, the sustained absence of pups may signal an opportunity to compete for a breeding position and pursue direct, rather than indirect, fitness.

NOTES

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