

Social suppression of female reproductive maturation and infanticidal behavior in cooperatively breeding Mongolian gerbils

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Abstract

In several cooperatively breeding species, reproductively suppressed, nonbreeding females are attracted to infants and routinely provide alloparental care, while breeding females may attack or kill other females' infants. The mechanisms underlying the transition from alloparental to infanticidal behavior are unknown. In this study, we tested the hypothesis that this transition is associated with cessation of reproductive suppression and onset of ovarian activity in the Mongolian gerbil (*Meriones unguiculatus*), a cooperatively breeding rodent. Young female gerbils were housed with their natal family (FH), with a female pairmate (PH) or singly (SH). When females were either 11–13 or 16–18 weeks of age, we characterized their behavioral responses to an unfamiliar pup, reproductive development, and plasma progesterone, cortisol, and prolactin concentrations. In both age groups, FH females were significantly less likely to attack pups than PH or SH females and in fact never did so. FH females also had smaller ovaries and uteri, less developed scent glands, and lower progesterone levels, and were more likely to be anovulatory than PH or SH females, especially in the 11- to 13-week-old age group. Prolactin concentrations did not differ with reproductive status but were significantly higher in females that did not attack pups than in those that did. We found no other significant associations, however, between reproductive or endocrine measures and behavioral responses to pups. These results suggest that cohabitation with the natal family inhibits both infanticidal behavior and reproductive maturation in young female gerbils but that these two effects may not be causally related.

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Introduction

Singular cooperative breeders are characterized by two unusual reproductive patterns (Emlen, 1991; Solomon and French, 1997). First, breeding in each social group is usually monopolized by a single, socially dominant female; behaviorally subordinate females typically undergo social suppression of reproduction, mediated by inhibition of sexual behavior and/or suppression of reproductive physiology. Second, nonbreeding individuals routinely provide care for the offspring of their dominant, breeding groupmates. This alloparental care may

involve such behaviors as provisioning, transporting, grooming, defending, and huddling with infants and may involve costs to the alloparents such as reduced time for foraging, decreased mobility, increased risk of predation, and energetic costs (Snowdon, 1996; Tardif, 1997). Nonetheless, providing alloparental care is generally thought to confer a net benefit to nonbreeders, in terms of increased direct and/or indirect fitness, and therefore to offset the fitness losses stemming from reproductive suppression (Brown, 1987, Emlen, 1991; Snowdon, 1996; Tardif, 1997).

It is becoming increasingly clear, however, that cooperative breeding may also be associated with high levels of aggression towards infants, especially by breeding females. In many singular cooperative breeding species, two or more females sometimes reproduce in the same group. Recent empirical

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studies indicate that the breeding females in such groups may occasionally or commonly kill each other's eggs or offspring in a wide variety of cooperative breeders, including social insects (Eggert and Müller, 2000; Keeping, 1992; Ratnieks and Visscher, 1989), birds (Mumme et al., 1983; Vehrencamp, 1977), rodents (Elwood, 1977, 1980, 1981), carnivores (Clutton-Brock et al., 1998; Corbett, 1988, Packer and Pusey, 1984; Rasa, 1987), and primates (Saltzman, 2003). Moreover, recent theoretical models suggest that infanticide by females can play a key role in promoting high reproductive skew in cooperatively breeding species (Hager and Johnstone, 2004) and may be an evolutionarily stable strategy (Tuomi et al., 1997). The common expression of both alloparental behavior by nonbreeders and infanticide by breeding females suggests that female cooperative breeders experience a tradeoff between indirect and direct reproduction, and that the onset of breeding is associated with a shift from alloparental to infanticidal behavior. A causal relationship between reproductive status and responses to infants has not been established, however, and the proximate mechanisms of the shift from alloparental to infanticidal behavior are not known.

To begin to characterize these mechanisms, we investigated the relationship between reproductive suppression and responses to pups in the Mongolian gerbil (*Meriones unguiculatus*), a cooperatively breeding cricetid rodent. Groups typically comprise a breeding pair, their pups, and several of their previous litters (Ågren, 1976; Ågren et al., 1989; Roper and Polioudakis, 1977; Swanson and Lockley, 1978). Both males and females may remain with their natal family for prolonged periods as non-reproductive alloparents, assisting with such parental duties as nest-building, licking pups, and huddling with pups (Ostermeyer and Elwood, 1984; Swanson and Lockley, 1978). The endocrine profiles of nonbreeding females have not been characterized directly, but females living with their parents, especially with their mothers, have been found to have atrophic uteri, small ovaries with no large follicles or corpora lutea, and minimal development of the gonadal-hormone-dependent ventral scent gland (Payman and Swanson, 1980, Swanson and Lockley, 1978). Other adult females, in contrast, undergo spontaneous estrous cycles lasting 4–6 days (Barfield and Beeman, 1968; Nishino and Totsukawa, 1996). These findings suggest that ovulation, ovarian hormone secretion, and pituitary gonadotropin secretion may be suppressed in response to cues from the natal family.

Cohabitation with the natal family may also influence females' responses to pups. In contrast to the alloparental behavior exhibited by females living with their natal family, adult female gerbils housed apart from their family are highly aggressive to unfamiliar pups. Elwood (1977, 1980, 1981) has shown that, when presented with unfamiliar pups, both nulliparous and parous females regularly commit infanticide unless they are in the late stages of pregnancy or the early to middle stages of lactation. These findings suggest that cues from the natal family, in addition to suppressing reproductive function, may promote alloparental responsiveness and inhibit infanticide in females.

In this study, we characterized reproductive development and responses to unfamiliar pups in female gerbils housed either with or away from their natal family, to determine whether cohabitation with the family inhibits infanticide and promotes alloparental behavior and, if so, whether this effect might be mediated by social suppression of reproduction. Because social isolation per se might increase aggressiveness (e.g., Brain and Nowell, 1971) and because cohabitation with a male or female pairmate might accelerate or delay reproductive maturation (Clark and Galef, 2001, 2002), we compared family-housed female gerbils both with singly housed females and with females that were pair-housed with a same-sex partner.

Methods

Animals

We used F1 descendants of gerbils purchased from Harlan (Indianapolis, IN). The Harlan colony is likely to be relatively inbred: it is derived from 5 female and 4 male founders, which were imported in 1954 from a random-bred colony descended from 20 pairs imported from Mongolia in 1935 (Brain, 1999). Harlan gerbils are random-bred, except that parent–offspring and sibling matings are avoided.

Animals were housed in clear polycarbonate cages (48 × 27 × 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 libitum, and supplements of carrots, oats, and sunflower seeds were each provided once per week. Lights were on from 07:00 to 19:00 h, and room temperature and humidity were maintained at approximately 23°C and 30–60%, respectively.

Design

Each of 78 female gerbils was assigned to one of three housing conditions (family-housed [FH], pair-housed [PH], or singly housed [SH]) and was tested at one of two ages (11–13 weeks [onset of adulthood; Marston and Chang, 1965; Thiessen and Yahr, 1977] or 16–18 weeks [young adult]). FH animals were housed continuously with their natal family, but, when the subjects were 48–57 days old, all littermates and older siblings were permanently removed. The mothers in these families gave birth to litters of 4–8 pups at approximately 32-day intervals; thus, FH females were housed with pups virtually continuously. Younger siblings were removed from the family as necessary to prevent crowding. The remaining subjects were removed from their families at 48–57 days of age and paired with a non-sibling, age-matched female. PH females remained with their female pairmate for the remainder of the experiment, whereas SH females were removed from their pairmate and housed alone in a new cage at least 6 days before undergoing a pup test and sacrifice. All PH and SH females were housed with pups (younger siblings) for at least 8 days (19 ± 1 days, mean ± SEM) prior to removal from the family.

Each week, beginning at 7–8 weeks of age, each female was weighed to the nearest gram, and her ventral scent gland was assessed using a 4-point scale as follows: 0—scent gland not visible; 1—pale yellow or pale orange coloration without distinct borders; 2—distinct yellow or orange coloration with distinct borders; 3—brown coloration with distinct borders. Each animal underwent a single pup test (see below) at either 11–13 ($N = 12$ FH, 16 PH, 14 SH) or 16–18 weeks of age ($N = 12$ FH, 12 PH, 12 SH) and was sacrificed the following morning for blood sample collection and reproductive tract assessment (see below).

Pup tests

Each female underwent a single pup test at 09:00–11:00 h. 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, 0–4 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 et al., 2000). 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 (that is, blood was observed on the pup or bedding) at any time, the test was terminated immediately and the pup was euthanized. When two pairmates (PH females) were tested the same day, we allowed at least 30 min to elapse from reunion of the pair, following the first animal's pup test, to the beginning of the second animal's test. All behavioral data were collected by a single observer. Behaviors scored included the test female sniffing, licking, mouthing (placing mouth on pup without biting aggressively), handling, approaching (moving to ≤ 5 cm of the pup), leaving (moving to >5 cm from the pup), crouching over (nursing posture), and retrieving the pup, and squealing performed by the pup. From these measures, we determined the total amount of time that the female spent in proximity to the pup, sniffing the pup, or licking the pup; the number of bouts of the female mouthing or handling the pup; and the number of bouts of the pup squealing.

Blood sampling and reproductive tract assessment

Animals were killed by CO₂ inhalation at 09:00–09:30 h the morning after undergoing a pup test, and blood was collected by cardiac puncture into a heparinized syringe. 97% of blood samples were collected within 2 min from initial exposure of the animal to CO₂, and 99% were collected within 3 min from initial disturbance to the animal. Samples were immediately placed on ice and centrifuged at 2600 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 and their scent glands measured and assessed. Ovaries and uteri were excised and cleaned of connective tissue, and their wet weights were determined to ± 0.0001 g. Ovaries were examined under a dissecting microscope, and the diameter of corpora lutea or of the largest follicles seen was recorded. Gerbils 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.

Hormone assays

Plasma cortisol concentrations were determined in duplicate aliquots by radioimmunoassay (RIA) using an antibody-coated tube kit (GammaCoat, DiaSorin, Stillwater, MN) following extraction with dichloromethane (DCM). To ensure that the incubation reached equilibrium, the protocol was modified to include overnight incubation at room temperature prior to aspiration of the liquid unbound portion (Saltzman et al., 1994). The protocol was further modified by extending the range of the standard curve to 0.1–15 ng/tube. The cortisol assay was fully validated for use with Mongolian gerbil plasma. Serial dilutions of a DCM-extracted gerbil plasma pool (12.00–1.50 μ l; $N = 8$) yielded a displacement curve parallel to that obtained with cortisol standards, and the recovery of cortisol standards added to 2 μ l DCM-extracted gerbil plasma was $93.79 \pm 1.69\%$ (mean \pm SEM; $N = 15$). Assay sensitivity at 90% binding was 0.063 ng/tube (31.5 ng/ml), and intra- and inter-assay coefficients of variation (CVs) of a plasma pool assayed in quadruplicate in each assay (33% binding) were 5.73% and 10.65%, respectively.

Plasma progesterone concentrations were determined in duplicate aliquots by enzyme immunoassay (EIA) using the methods of Saltzman et al. (1994), following extraction with petroleum ether. Serial dilutions of a gerbil plasma pool (5.42–0.17 μ l; $N = 6$) yielded a displacement curve parallel to that obtained with progesterone standards (Sigma, St. Louis, MO). The recovery of progesterone standards added to 5 μ l of a gerbil plasma pool was $107.17 \pm 2.13\%$ (mean \pm SEM; $N = 8$). The sensitivity of the assay at 90% binding was 4.1 pg/tube (0.82 ng/ml), and intra- and inter-assay CVs of a plasma pool assayed in quadruplicate on each plate (59% binding) were 3.37% and 18.33%, respectively.

Plasma prolactin concentrations were measured using the National Hormone and Peptide Program's hamster prolactin RIA (Dr. A.F. Parlow; Harbor-UCLA Medical Center, Torrance, CA), as used routinely in several species of hamsters (e.g., Edwards et al., 1995; Lewis et al., 2002). Because plasma volumes were

limited, only a single aliquot of each sample was assayed. All samples were run in a single assay, using a plasma volume of 120 μ l. Additional information on assay methodology and validation is available from Dr. Parlow. Because this assay is not in routine use in this species, we analyzed prolactin data using nonparametric statistics. For convenience, results are reported as ng/ml prolactin; however, because the assay reagents were developed for golden hamsters, the units should more appropriately be interpreted as ng-equivalents hamster prolactin/ml.

Data analysis

Three family-housed subjects sustained pregnancies during the study; data from these animals were omitted from analyses of body mass, uterine mass, and ovarian mass. Because uterine and ovarian mass may be expected to correlate with body mass, uterine and ovarian masses were analyzed by analysis of covariance, using age and body mass at sacrifice as covariates (SAS v. 8 PROC MIXED, SAS Institute, Cary, NC, 2000). Uterine mass, ovarian mass, and body mass were log-transformed to increase normality. Analyses were initially performed with all interaction terms included; nonsignificant interactions were subsequently omitted and analyses rerun. When analyses yielded significant differences among housing conditions, we subsequently performed pairwise comparisons using a similar ANCOVA design. Body mass was analyzed by ANOVA, and post hoc comparisons following significant ANOVA results were performed by Tukey tests.

Reproductive status (ovulatory vs. anovulatory) and agonistic responses to pups (aggressive vs. non-aggressive) were analyzed using χ^2 tests. To determine whether ovulatory females were more likely to behave aggressively toward pups than were anovulatory females, we performed a series of 2 (ovulatory vs. anovulatory) \times 2 (aggressive vs. not aggressive) χ^2 tests. For each age group, we first performed one analysis using females from all three housing conditions. Because ongoing interactions with pups (younger siblings) might have obscured the relationship between ovarian status and responses to pups in FH females, we also analyzed the data from each age group using only SH and PH females.

Scent gland development scores, plasma hormone concentrations, and non-agonistic behaviors in pup tests were not normally distributed and therefore were analyzed nonparametrically by Kruskal–Wallis tests, Mann–Whitney U tests, and nonparametric multiple-comparison tests (Zar, 1999). Nonparametric tests and ANOVAs were performed using Systat v. 5 for the Macintosh (Chicago, IL). All analyses were assessed using a critical P value of 0.05 (2-tailed).

Results

Behavioral responses to pups

In 31 of the 78 pup tests, the female attacked the pup, necessitating early termination of the test. The proportion of females attacking pups differed among the three housing conditions in each age group (11–13 weeks old: $\chi^2 = 12.06$, $df = 2$, $P < 0.01$; 16–18 weeks old: $\chi^2 = 20.28$, $df = 2$, $P < 0.001$; Table 1). No family-housed (FH) females attacked pups, whereas many pair-housed (PH) and most singly housed (SH) females did so.

To further evaluate the effects of housing condition on females' responses to pups, we compared behaviors in pup tests among those FH, PH, and SH females that did not attack pups. Because relatively few PH and SH females were non-aggressive toward pups, we combined data from the two age groups for each housing condition. Results are summarized in Table 2. Total time spent in proximity (≤ 5 cm) to the pup differed significantly across housing conditions: FH females spent less time in proximity than did PH females, and SH females spent an intermediate amount of time in proximity to the pup. FH

Table 1
Aggression toward unfamiliar pups, body mass, reproductive development, and hormone levels in family-housed (FH), pair-housed (PH), and singly housed (SH) female gerbils assessed at either 11–13 or 16–18 weeks of age

Measure	Age (weeks)	FH	PH	SH	<i>P</i>
Proportion aggressive in pup test	11–13	0/12 (0%)	5/16 (31.3%)	9/14 (64.3%)	<0.01 ^a
	16–18	0/12 (0%)	6/12 (50.0%)	11/12 (91.7%)	<0.001 ^a
Proportion ovulatory ^b	11–13	3/12 (25.0%)	14/16 (87.5%)	8/14 (57.1%)	<0.01 ^a
	16–18	5/12 (41.7%)	10/12 (83.3%)	9/12 (75.0%)	0.1 > <i>P</i> > 0.05 ^a
Body mass at sacrifice (g; antilog of mean, 95% conf. limits)	11–13	49.1 (51.4, 46.9)	51.6 (53.8, 49.5)	51.6 (53.8, 49.6)	>0.2 ^c
	16–18	52.6 (56.0, 49.4)	56.1 (58.3, 54.0)	58.2 ^d (61.7, 54.9)	0.046 ^c
Scent gland score at sacrifice (mean ± SEM)	11–13	1.3 ± 0.8	2.7 ± 0.7 ^c	2.6 ± 0.8 ^c	0.001 ^f
	16–18	1.6 ± 1.1	3.0 ± 0.0 ^g	2.9 ± 0.3 ^c	<0.001 ^f
Uterine mass (mg; antilog of mean, 95% conf. limits)	11–13	68.6 (96.1, 48.9)	125.6 ^c (144.6, 109.1)	135.8 ^d (173.1, 106.6)	0.004 ^h
	16–18	74.6 (116.7, 47.8)	167.1 (211.3, 132.2)	185.4 (238.3, 144.2)	0.075 ^h
Total ovarian mass (mg; antilog of mean, 95% conf. limits)	11–13	15.1 (18.5, 12.3)	22.4 ^c (25.2, 19.9)	20.0 (23.7, 16.8)	0.028 ^h
	16–18	16.0 (20.2, 12.7)	23.1 (27.3, 19.6)	23.6 (27.0, 20.6)	0.011 ^h
Plasma progesterone (ng/ml; median, range)	11–13	2.01 (1.43–71.38)	14.91 ^c (2.73–128.13)	6.05 (1.62–15.65)	0.012 ^f
	16–18	3.88 (0.82–79.94)	19.02 (4.39–89.70)	10.89 (1.99–56.03)	0.080 ^f
Plasma cortisol (ng/ml; median, range)	11–13	38.5 (31.5–64.9)	31.5 ^{d,i} (31.5–139.8)	39.1 (31.5–131.6)	0.014 ^f
	16–18	48.0 (31.5–160.7)	37.8 (31.5–84.2)	31.5 (31.5–118.1)	>0.4 ^f
Plasma prolactin (ng/ml; median, range)	11–13	0.9 (0.2–1.7)	1.1 (0.2–5.0)	0.6 (0.2–1.9)	>0.2 ^f
	16–18	0.9 (0.5–3.9)	0.9 (0.4–4.3)	0.5 ^d (0.2–2.3)	0.021 ^f

^a From χ^2 test comparing FH, PH, and SH females (pairwise comparisons not performed).

^b Includes 2 pregnant FH females (one in each age group) and one postpartum FH female (16–18 weeks).

^c From ANOVA comparing FH, PH, and SH females.

^d *P* < 0.05, compared to FH.

^e *P* < 0.01, compared to FH.

^f From Kruskal–Wallis test comparing FH, PH, and SH females.

^g *P* ≤ 0.001, compared to FH.

^h Main effect of housing condition from ANCOVA comparing FH, PH, and SH females. See text for further details.

ⁱ *P* < 0.05, compared to SH.

females also spent less time sniffing the pup and performed fewer bouts of mouthing pups than did either PH or SH females; however, mean proportion of time spent licking the pup did not differ across housing conditions. The number of bouts of females handling pups differed reliably across housing conditions, but pairwise comparisons were not significant. Pups performed fewer bouts of squealing with FH females than with either PH or SH females. Other behaviors (retrieve pup, crouch over pup) occurred too infrequently to permit analysis.

Body mass

Body mass increased with age as expected [11- to 13-week-old group: $F(3,114) = 194.30$, $P < 0.001$; 16- to 18-week-old group: $F(7,217) = 167.98$, $P < 0.001$; Fig. 1]. In the younger age group, body mass did not differ among housing conditions across weeks of age (main effect of condition: $P > 0.3$, condition × week interaction: $P > 0.6$) or at the time of sacrifice ($P > 0.2$). In the older age group, body mass differed reliably at

Table 2
Behavior scores (median, range) in 10-min pup tests of family-housed (FH), pair-housed (PH), and singly housed (SH) female gerbils, including both 11- to 13- and 16- to 18-week-old animals, that were not aggressive to pups

Behavior	FH	PH	SH	<i>P</i> ^a
Proximity to pup (% of total time)	23.8 (3.4–48.1)	42.1 ^b (13.5–90.1)	34.2 (29.3–41.4)	<0.001
Sniff pup (% of total time)	10.1 (2.0–39.0)	20.9 ^b (6.3–50.2)	17.0 ^c (13.6–24.1)	<0.001
Mouth pup (no. of bouts)	0.0 (0–1)	4.0 ^b (0–13)	4.5 ^b (2–12)	<0.001
Handle pup (no. of bouts)	9.5 (1–22)	13.0 (6–29)	14.0 (9–16)	0.036
Squealing by pup (no. of bouts)	0.0 (0–3)	3.0 ^b (0–12)	5.0 ^b (3–9)	<0.001
Lick pup (% of total time)	0.8 (0.0–81.5)	0.7 (0.0–11.3)	0.0 (0.0–33.5)	>0.5

^a From Kruskal–Wallis test comparing FH, PH, and SH females.

^b *P* < 0.001, compared to FH.

^c *P* < 0.05, compared to FH.

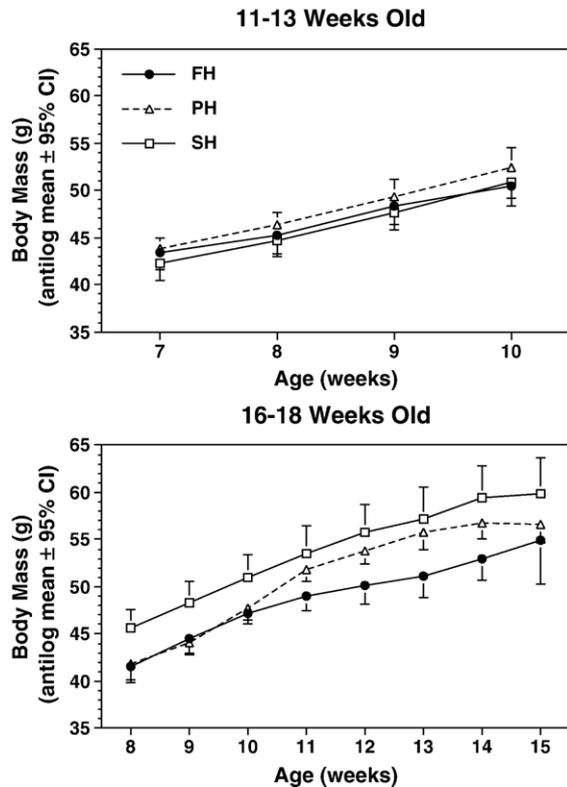


Fig. 1. Body mass (antilog of mean \pm 95% confidence intervals) of family-housed (FH), pair-housed (PH), and singly housed (SH) female gerbils across weeks of age. See text for statistical results.

7–8 weeks of age, when animals were first placed in their respective housing conditions [$F(2,24) = 8.82, P = 0.001$], as SH females were heavier than both FH ($P = 0.008$) and PH females ($P = 0.003$). Subsequent changes in body mass over weeks of age differed among the three housing conditions in the older age group [main effect of condition: $F(2,31) = 6.40, P = 0.005$, condition \times week interaction: $F(14,217) = 1.80, P = 0.039$], as FH females gained mass more slowly than did PH and SH females (Fig. 1). Consequently, body mass at the time of sacrifice differed among housing conditions in the 16- to 18-week-old group [$F(2,31) = 3.40, P = 0.046$], with FH females having significantly lower body mass than SH females ($P = 0.038$) and PH females intermediate (Table 1).

Scent gland development

Patterns of scent gland development over time differed among housing conditions (Fig. 2). In the 11- to 13-week-old group, scent gland development did not differ until gerbils were 10 (Kruskal–Wallis $H = 10.00, df = 2, P = 0.007$) and 11 (Kruskal–Wallis $H = 8.32, df = 2, P = 0.016$) weeks of age. At 10 weeks of age, FH females had significantly lower scent gland scores than both PH ($P < 0.02$) and SH females ($P < 0.02$), whereas at 11 weeks of age they differed only from PH females ($P < 0.02$). In the 16- to 18-week-old group, scent gland development did not differ among housing conditions at 7 weeks of age ($P > 0.1$) but did so at all subsequent ages (Kruskal–Wallis $H = 7.12–22.00, df = 2, P$'s < 0.05). Beginning

at 10 weeks of age, FH females had significantly lower scent gland scores than both PH and SH females (P 's < 0.05). In both age groups, most FH females showed little or no development of the scent gland at the time of sacrifice, whereas most SH and PH females showed maximal scent gland development (P 's ≤ 0.001 ; Table 1).

Reproductive development

Uterine mass differed among housing conditions in the 11- to 13-week-old group [$F(2,36) = 6.34, P = 0.004$; Table 1, Fig. 3] and was marginally affected by body mass [$F(1,36) = 3.62, P = 0.065$]. Pairwise analyses revealed that uterine mass was lower in FH females than in both PH ($P = 0.005$) and SH females ($P = 0.014$) but did not differ between PH and SH animals ($P > 0.5$). In the 16- to 18-week-old group, uterine mass tended to differ among housing conditions [$F(2,27) = 2.86, P = 0.075$; Table 1, Fig. 3] and to be influenced by body mass at sacrifice [$F(1,27) = 4.02, P = 0.055$] as well as by the interaction between housing condition and body mass [$F(2,27) = 2.67, P = 0.087$]. Pearson correlations performed separately on each housing condition within the 16- to 18-week-old age group indicated that uterine mass was significantly correlated with body mass among FH females ($R = 0.724, P = 0.018$) but not among PH ($R = 0.120, P > 0.7$) or SH females ($R = 0.019, P > 0.9$). Uterine mass was not significantly affected by age within either age group (P 's > 0.3).

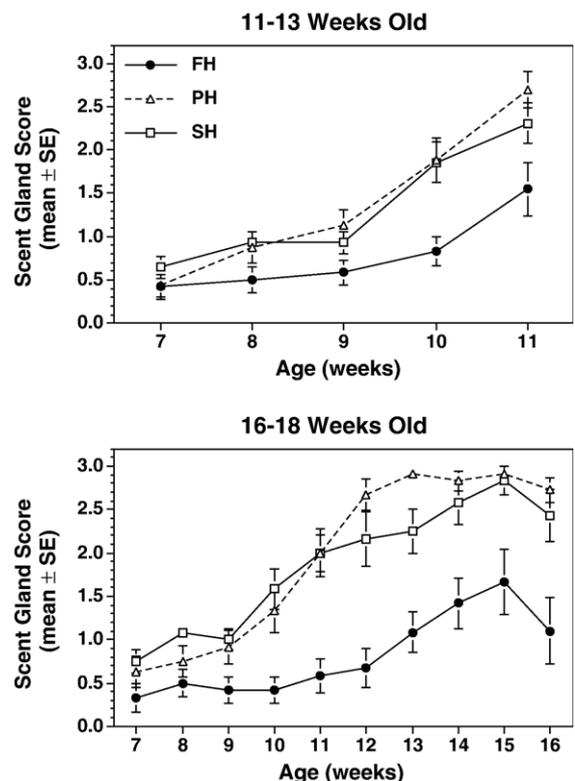


Fig. 2. Scent gland scores (mean \pm SEM) of family-housed (FH), pair-housed (PH), and singly housed (SH) female gerbils across weeks of age. See text for statistical results.

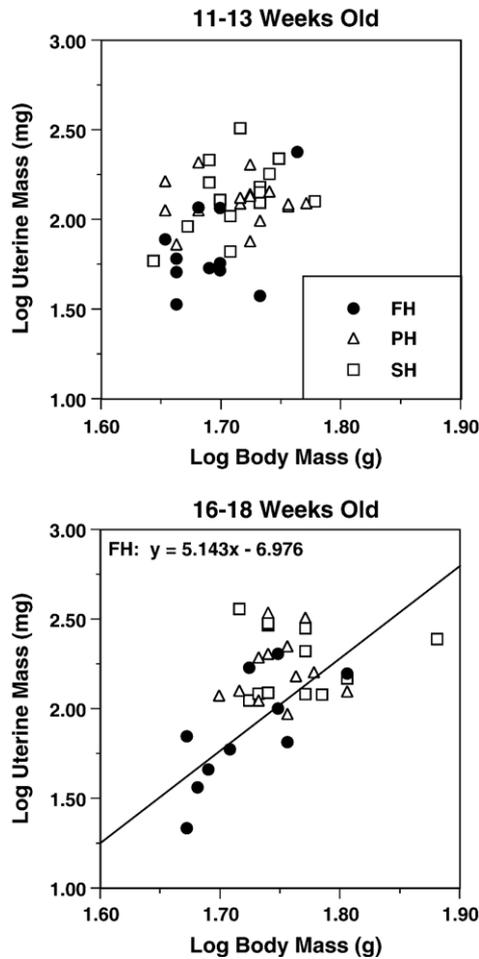


Fig. 3. Log of uterine mass vs. log of body mass for family-housed (FH), pair-housed (PH), and singly housed (SH) female gerbils at 11–13 or 16–18 weeks of age. Regression line (lower graph) is for FH females. See text for statistical results.

Total ovarian mass in 11- to 13-week-old females differed among housing conditions [$F(2,36) = 3.94$, $P = 0.028$; Table 1, Fig. 4] and was affected by body mass [$F(1,36) = 29.28$, $P < 0.001$]. Pairwise analyses revealed that ovarian mass was lower in FH females than in PH females ($P = 0.005$) but not SH females ($P > 0.2$) and did not differ between PH and SH animals ($P > 0.1$). Among 16- to 18-week-old animals, ovarian mass differed among housing conditions [$F(2,27) = 5.34$, $P = 0.011$; Table 1, Fig. 4] and was affected by body mass [$F(1,27) = 6.62$, $P = 0.016$] as well as by the interaction between housing condition and body mass [$F(2,27) = 5.14$, $P = 0.013$]. Subsequent Pearson correlations conducted separately on each housing condition in the 16- to 18-week-old group indicated that ovarian mass, like uterine mass, correlated significantly with body mass among FH females ($R = 0.884$, $P < 0.001$) but not among PH ($R = 0.169$, $P > 0.5$) or SH females ($R = 0.120$, $P > 0.7$). Ovarian mass was not significantly affected by age within either age group (P 's > 0.1).

The proportion of females that were ovulatory (or pregnant/postpartum) vs. anovulatory differed across housing conditions in the 11- to 13-week-old group ($\chi^2 = 11.17$, $df = 2$, $P < 0.01$; Table 1) and tended to differ in the 16- to 18-week-old group

($\chi^2 = 5.25$, $df = 2$, $0.1 > P > 0.05$). In both age groups, most FH females had no corpora lutea or large follicles and were therefore considered anovulatory, whereas most SH and PH females had corpora lutea and/or large follicles, indicative of ovulatory activity. Two FH females (one in each age group) were pregnant, and one (16–18 weeks old) had given birth the day before being sacrificed.

Progesterone

Plasma progesterone concentrations differed among housing conditions in the 11- to 13-week-old animals (Kruskal–Wallis $H = 8.92$, $df = 2$, $P = 0.012$; Table 1). Post hoc tests revealed that progesterone levels were significantly higher in PH than in FH animals ($P < 0.01$) and were intermediate in SH animals. Progesterone concentrations also tended to differ among housing conditions in the 16- to 18-week-old animals, with FH animals having lower levels than the other groups; however, this trend was not statistically significant (Kruskal–Wallis $H = 5.05$, $df = 2$, $P = 0.080$, Table 1). Overall, as expected, progesterone concentrations were higher in females whose

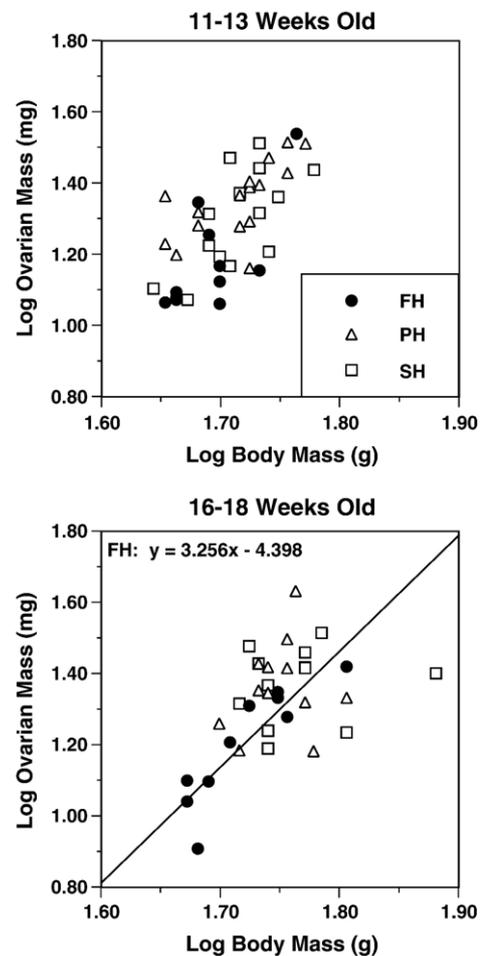


Fig. 4. Log of total ovarian mass vs. log of body mass for family-housed (FH), pair-housed (PH), and singly housed (SH) female gerbils at 11–13 or 16–18 weeks of age. Regression line (lower graph) is for FH females. See text for statistical results.

ovaries contained large follicles and/or corpora lutea at sacrifice ($N = 46$, excluding pregnant and postpartum females) than in those whose ovaries contained only small follicles [$N = 29$; 13.28 (3.40–128.13) vs. 2.23 (0.44–15.65) ng/ml, respectively; median (range); Mann–Whitney $U = 77.0$, $N = 75$, $P < 0.001$].

Cortisol

Plasma cortisol levels differed among housing conditions in the 11- to 13-week-old group (Kruskal–Wallis $H = 8.51$, $df = 2$, $P = 0.014$; Table 1). Post hoc tests indicated that cortisol was lower in PH females than in either FH ($P < 0.05$) or SH females ($P < 0.05$) but did not differ between the latter two conditions. Cortisol concentrations did not differ among housing conditions in the 16- to 18-week-old animals ($P > 0.4$). For all groups combined, cortisol levels were higher in anovulatory females than in ovulatory females [42.5 (31.5–160.7) vs. 31.5 (31.5–131.6) ng/ml, respectively; median (range); Mann–Whitney $U = 1002.0$, $N = 75$, $P < 0.001$]. When ovulatory and anovulatory females were analyzed separately, combining data from both age groups, no differences in cortisol levels were found among FH, PH, and SH females (P 's > 0.7).

Prolactin

Circulating prolactin concentrations did not differ among FH, PH, and SH animals in the 11- to 13-week-old group ($P > 0.2$; Table 1) but did in the 16- to 18-week-old group (Kruskal–Wallis $H = 7.74$, $P = 0.021$) as SH animals had significantly lower prolactin levels than FH animals ($P < 0.05$) and marginally lower prolactin levels than PH animals ($0.1 > P > 0.05$). Prolactin levels did not differ between ovulatory and anovulatory females ($P > 0.1$).

Relationships between reproductive development and responses to pups

χ^2 tests indicated that gerbils' reproductive status (ovulatory vs. anovulatory) was not reliably associated with their responses to unfamiliar infants (aggressive vs. not aggressive) in either age group, whether we included all females or only PH and SH females in the analyses (see Fig. 5). When animals from all three housing conditions and both age groups were analyzed together, gerbils that attacked pups had significantly heavier uteri [$T(73) = -3.16$, $P = 0.002$] and tended to have heavier ovaries [$T(73) = -1.72$, $P = 0.089$] than those that did not attack pups. These difference disappeared, however, when FH females were excluded from the analyses (P 's > 0.4).

For all animals considered together, neither plasma progesterone ($P > 0.4$) nor plasma cortisol concentrations ($P > 0.2$) differed reliably between females that did and those that did not attack unfamiliar pups. When FH females were omitted from the analyses, progesterone ($P > 0.1$) and cortisol ($P > 0.7$) again failed to differ between females that did and did not attack pups. Plasma prolactin levels, in contrast, were higher in females that did not attack pups than in those that did, when all animals were analyzed together [1.00 (0.20–5.00) vs. 0.50 (0.20–2.50) ng/

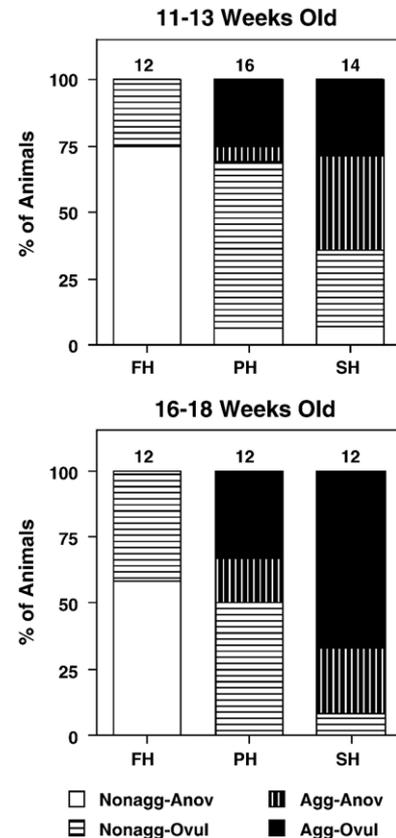


Fig. 5. Relationships among housing condition, aggression in pup tests, and ovulatory status in 11- to 13- and 16- to 18-week-old female gerbils that were family-housed (FH), pair-housed (PH), or singly housed (SH). Numbers above bars indicate sample sizes. Solid bars indicate proportions of gerbils showing the expected associations between anovulation and absence of aggression toward pups (white bars) or ovulatory activity and aggression toward pups (black bars). Hatched bars indicate proportions of gerbils showing unexpected associations of anovulation with aggression toward pups (vertically hatched bars) or ovulatory activity with absence of aggression (horizontally hatched bars). FH females were less likely than PH and SH females to attack pups and to be classified as ovulatory, but ovulatory females were not more likely to attack pups than were anovulatory females. For clarity, data are shown separately for each housing condition; in analyses, however, data were combined across housing conditions.

ml, respectively; median (range); Mann–Whitney $U = 1021.5$, $N = 78$, $P = 0.003$] as well as when FH females were omitted from the analysis [1.00 (0.20–5.00) vs. 0.50 (0.20–2.50) ng/ml, respectively; Mann–Whitney $U = 480.5$, $N = 54$, $P = 0.030$].

Discussion

The results of this study confirm that cohabitation with the natal family inhibits physiological reproductive development in female Mongolian gerbils and demonstrate, for the first time, that it also inhibits the expression of infanticide. These two effects of cohabitation with the natal family do not, however, appear to be closely linked. Thus, the age-related increase in infanticidal behavior that has been reported in female gerbils (Elwood, 1980) and the contrasting responses to pups by group-housed breeding and nonbreeding females (cf. Elwood 1977, 1981; Ostermeyer and Elwood, 1984) do not appear to be mediated by the onset of ovulatory cyclicity.

Social influences on responses to pups

Our results confirm previous findings that adult female gerbils housed away from their natal family are highly aggressive toward unfamiliar pups (Elwood, 1977, 1980, 1981). Most of the PH and SH females in our study attacked pups, and this effect was seen as early as 11–13 weeks of age, corresponding to the onset of adulthood (Marston and Chang, 1965; Thiessen and Yahr, 1977). Elwood (1980) found that female gerbils became increasingly aggressive towards unfamiliar pups with age until, by 6 months of age, virtually all females killed pups. Infanticidal behavior was inhibited only during the early to middle stages of lactation and final days of pregnancy (Elwood, 1977, 1981), even in experienced breeders.

We have shown in the present study that infanticide by female gerbils is additionally inhibited by continuous cohabitation with the natal family: none of the 24 females housed with their family attacked unfamiliar pups. Interestingly, however, non-aggressive females did not exhibit distinct maternal behaviors in pup tests. For example, none of the animals crouched over the pup in a nursing posture, and only three, including two aggressive females, retrieved the pup. Furthermore, FH females sniffed and handled pups less than did non-aggressive PH and SH females and spent less time in proximity to pups. These differences may reflect the fact that FH females had been housed with pups virtually continuously since about 1 month of age, whereas PH and SH females had not been housed with pups for at least 4 (11- to 13-week-old condition) or 8 weeks (16- to 18-week-old condition) prior to pup testing and therefore may have responded to them as a novel stimulus.

Inhibition of infanticide in FH females could have been mediated by their continuing interactions with younger siblings and/or by continuous cohabitation with the parents. Both factors have been found to influence alloparental and aggressive responses to pups in other cooperatively breeding rodents. In virgin female prairie voles (*Microtus ochrogaster*), continuous housing with the natal family increased alloparental responsiveness and decreased aggression toward unfamiliar pups (Lonstein and De Vries, 2001). Housing with both parents enhanced alloparental behavior to a greater extent than did housing with either the mother or father separately. The effect of the parents on alloparental responsiveness in virgin female prairie voles was not dependent upon experience with younger siblings (Lonstein and De Vries, 2001), but Roberts et al. (1998) found that alloparental responsiveness in subadult and juvenile prairie voles of both sexes was enhanced by previous experience with pups. Among California mice (*Peromyscus californicus*), in contrast, housing with the parents and younger siblings, but not with the parents alone, increased parental responses to foster pups in young juvenile males and females; however, this effect disappeared at approximately the age of onset of sexual maturity (Gubernick and Laskin, 1994). Notably, all female gerbils in the present study had been housed with younger siblings for at least 8 days. Thus, previous experience with pups does not permanently inhibit infanticidal behavior in nonbreeding female gerbils.

Social influences on reproductive maturation

Our results confirm previous findings that female Mongolian gerbils undergo suppression of reproductive physiology while housed with their natal family (Swanson and Lockley, 1978). At the time of sacrifice, FH females had lower plasma progesterone levels and were less likely to have large follicles or corpora lutea than SH and PH females, although these differences were significant only in the younger age group. Furthermore, in both age groups, development of the ventral scent gland was inhibited in FH females compared to females housed away from their natal family. This difference is likely to reflect low circulating levels of estrogens (and perhaps androgens) in FH females, as scent glands of female Mongolian gerbils have been reported to become significantly smaller or even undetectable following ovariectomy, whereas scent gland development can be reinstated by treatment with estrogen, estrogen + progesterone, or androgens (Wallace et al., 1973; Yahr and Thiessen, 1975).

FH females also tended to have smaller ovaries and uteri than PH and SH females. Among 11- to 13-week-old gerbils, both ovarian and uterine mass were positively correlated with body mass at the time of sacrifice, and these relationships did not differ among the three housing conditions; however, FH females had significantly lower uterine masses than both PH and SH females and significantly lower ovarian masses than PH females. Among 16- to 18-week-old animals, in contrast, both ovarian and uterine mass were positively correlated with body mass in FH but not PH or SH females. Body mass also differed among housing conditions in the older age group, with FH females having significantly lower body mass than SH females. These findings suggest that reproductive maturation in 11- to 13-week-old gerbils was associated with overall physical maturation, as reflected in body size, and that animals in all three housing conditions were maturing at this age, although FH females lagged behind PH and SH females. Among 16- to 18-week-old animals, in contrast, most PH and SH females appear to have reached full physical and reproductive maturity, so that no further relationship was apparent between body mass and ovarian or uterine mass, whereas FH females showed continuing physical and reproductive development. Thus, cohabitation with the family retards but does not prevent reproductive maturation in female gerbils. Correspondingly, Clark and Galef (2001, 2002) found that cohabitation with family members or with other familiar individuals delays the time of first parturition but does not usually alter the probability that young females will breed by 16.5 weeks of age.

Although several previous studies have found that female gerbils usually do not breed while housed with their natal family (French, 1994; Payman and Swanson, 1980; Swanson and Lockley, 1978), few have examined the mechanisms of this reproductive failure. As in the present study, Swanson and Lockley (1978) found that many adult-aged daughters housed with their natal family exhibited no development of the ventral scent gland; small, atrophic uteri similar to those of ovariectomized females; and small, immature ovaries containing no large follicles or corpora lutea. Following separation from their

mother, however, daughters frequently initiated scent gland development and conceived. In conjunction with these previous findings, our results suggest that cues from the natal family may suppress follicular development, ovarian hormone secretion, and ovulation, possibly secondary to suppression of gonadotropin secretion from the pituitary, as has been demonstrated in several other cooperatively breeding mammals (e.g., common marmoset, *Callithrix jacchus*: Abbott et al., 1981; cotton-top tamarin, *Saguinus oedipus*: Ziegler et al., 1987; naked mole-rat, *Heterocephalus glaber*: Faulkes et al., 1990; Damaraland mole-rat, *Cryptomys damarensis*: Bennett et al., 1994; pine vole, *Microtus pinetorum*: Solomon et al., 2001). Clearly, however, the occurrence of this suppression is variable, as 8 of 24 FH females showed evidence of ovulatory activity and three of these females conceived. Other investigators have similarly reported that a small proportion of female gerbils breed while housed with their natal family (French, 1994; Payman and Swanson, 1980; Swanson and Lockley, 1978). Clark and Galef (2001, 2002), in contrast, found that many or most females gave birth by 16.5 weeks of age while housed with their biological or foster parents. In these studies, however, the females' younger siblings were removed immediately after birth (Clark and Galef, 2001, 2002), whereas Payman and Swanson (1980) found that young female gerbils housed with their mother and littermate sisters underwent reproductive suppression only if younger siblings were present.

The finding that plasma cortisol levels were higher in anovulatory than ovulatory females was unexpected. In a number of other singular cooperative breeders, studied in both the laboratory (Saltzman et al., 1994, 1998) and the field (Creel, 2001; Goymann and Wingfield, 2004), circulating or excreted glucocorticoid levels are higher in dominant, breeding females (and sometimes males) than in nonbreeding subordinates. These findings have been attributed to subordinate individuals in these societies experiencing less psychosocial stress or lower allostatic load than dominants (Abbott et al., 2003; Creel, 2001; Goymann and Wingfield, 2004; Sapolsky, 2005) or to low glucocorticoid levels in subordinate animals being mediated in part by low levels of reproductive hormones, especially in species in which subordinate individuals undergo social suppression of reproduction (Saltzman et al., 1994, 1998, 2000). Our finding of elevated cortisol concentrations in reproductively suppressed female gerbils, in contrast, could indicate that anovulation and delayed reproductive development were stress-induced. Because cortisol levels were not reliably higher in FH females than in PH and SH females, however, even when controlling for reproductive status, such stress effects would clearly not be specific to the socially induced reproductive suppression seen most consistently in FH females.

Another possibility is that high cortisol levels in anovulatory females were a consequence, rather than a cause, of reproductive suppression. In contrast to numerous rodent and primate species, in which estrogen elevates activity of the hypothalamic–pituitary–adrenal axis (reviewed by Saltzman et al., 1998; Wilson et al., 2005), ovarian hormones appear to *inhibit* adrenocortical activity in the

Mongolian gerbil: Nickerson (1975a,b) found that ovariectomy markedly increased adrenal mass and plasma cortisol levels and induced ultrastructural changes in the adrenal cortex indicative of hyperactivation, whereas estrogen treatment did not significantly elevate plasma cortisol concentrations. In our study, therefore, low levels of ovarian steroids may have stimulated or disinhibited cortisol secretion in anovulatory females.

Relationships among reproductive status, endocrine function, and responses to pups

Although female gerbils housed with their natal family showed both suppression of reproductive maturation and inhibition of infanticidal behavior toward unfamiliar pups, we found no evidence that these two effects were closely or causally linked. First, for all housing conditions analyzed together, as well as only for females housed away from their natal family, the occurrence of ovulatory activity was not significantly associated with aggression toward pups. Second, circulating concentrations of progesterone and cortisol did not differ between females that attacked pups and those that did not. Plasma prolactin concentrations, in contrast, were reliably lower in animals that attacked pups; however, prolactin levels did not differ between ovulatory and anovulatory females, suggesting that the association between prolactin and responses to pups was not mediated by differences in reproductive maturation.

Prolactin has been found to be positively associated with alloparental behavior in a number of avian and mammalian cooperative breeders (reviewed by Ziegler, 2000). As in the present study, most of these findings have been correlational; however, Roberts et al. (2001a) reported that pharmacological suppression of prolactin secretion inhibited alloparental responsiveness in cooperatively breeding marmoset monkeys. Thus, individual differences in circulating prolactin levels may have contributed to differences in behavioral responses to pups among female gerbils in our study. Alternatively, differences in gerbils' prolactin levels at the time of sacrifice could have been a consequence of differences in their interactions with pups the previous day. In marmosets, engaging in alloparental behavior (i.e., carrying infants) appears to stimulate prolactin secretion in nonbreeding males and females (Roberts et al., 2001b). Prolactin levels in marmosets were elevated immediately after bouts of infant-carrying, however, whereas prolactin differences in our study were detected 24 h after pup tests. Moreover, although prolactin levels of FH females were higher than those of SH animals in the older age group, the finding that prolactin levels were not consistently higher in FH gerbils (all of which were housed with pups up to the time of blood sampling) than in both PH and SH animals in both age groups suggests that ongoing interactions with pups are not a major determinant of circulating prolactin levels in nonbreeding female gerbils. Notably, Brown et al. (1995) found that male gerbils exhibited an increase in circulating prolactin levels following the birth of their first set of pups, but this increase did not become statistically significant until 11–20 days after parturition.

In contrast to prolactin, effects of ovarian hormones on responses to infants have received little attention in studies of cooperative breeders. In one study, however, estrogen treatment tended to reduce the frequency of infanticide and promote alloparental behavior in ovariectomized, virgin female prairie voles (Lonstein and De Vries, 1999). Notably, prairie voles do not undergo ovarian cyclicity or spontaneous ovarian activity or ovulation (Carter and Roberts, 1997), so this finding may not be highly relevant to the naturally occurring behavior of nonbreeding females. Alloparental behavior by young female prairie voles can also be enhanced by perinatal treatment with corticosterone (Roberts et al., 1996) but does not correlate acutely with endogenous corticosterone or luteinizing hormone levels (Roberts et al., 1998).

In summary, our findings demonstrate that infanticidal behavior by young adult female gerbils can be inhibited by cohabitation with the natal family but suggest that this effect is not closely linked to social inhibition of reproductive maturation. Instead, responses of nonbreeding females to pups may be more closely associated with circulating prolactin concentrations, which, again, do not correlate with reproductive status. Thus, although female gerbils and other cooperative breeders undergo a shift in their responses to nondescendant infants, from benign or alloparental behavior in nonbreeding females to infanticidal behavior in breeding females, this transition does not appear to be mediated by the termination of reproductive suppression and onset of ovulatory activity.

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