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Effects of Consanguinity, Exposure to Pregnant Females, and Stimulation from Young on Male Gerbils' Responses to Pups

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ABSTRACT: *In three experiments investigating variables affecting responses of male Mongolian gerbils to conspecific young, we compared the behavior directed towards pups of natural fathers, virgin foster fathers, and sexually experienced foster fathers (Experiment 1); males either previously exposed or not exposed to pregnant females (Experiment 2); and males provided or not provided with extra opportunities to huddle over pups (Experiment 3). We found no difference in responses to pups among natural fathers, virgin foster fathers, and foster fathers that had fathered litters. On the other hand, both a week of exposure to a pregnant female and opportunity to huddle over pups for an extra 15 min/day had significant effects on males' subsequent responses to conspecific young. We speculate on the reasons why a male's response to pups might be affected by his exposure to a pregnant female and stimuli from pups, but not by the probability that the pups were his own offspring.*
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Male Mongolian gerbils (*Meriones unguiculatus*) in our laboratory respond positively to conspecific young 2 to 20 days of age by licking, retrieving, and huddling over them when the pups' dam is away from the nest. On the day of pup birth, males are more ambiguous in their responses to young than they are on subsequent days (Clark & Galef, 1999, 2000a; Clark, Vonk, & Galef, 1998).

Although male gerbils in our studies were rarely infanticidal, even towards newborns, as were male gerbils examined by Elwood (1977, 1980), the males we observed did appear uncomfortable in the presence of neonates (Clark & Galef, 2000a) and ambivalent in their response to them. For example, on the day of birth of a litter, males frequently entered the nest box containing the litter and then withdrew—a behavior that completely disappeared by the time pups were 24 hr old (Clark & Galef, 2000a).

The design of our earlier studies required that we measure responses of male gerbils to foster litters, and often, for convenience, we used virgin males as foster fathers. Results of studies of experiential effects on parental behavior of male house mice (*Mus domesticus*) as well as male Mongolian gerbils suggest that interaction with females can affect males' subsequent responses to young, even inhibiting the normally infanticidal response males sometimes exhibit toward unfamiliar neonates (Elwood, 1977, 1980; vom Saal, 1985). Such experiential effects on

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parental behavior of male rodents suggest that the low levels of paternal response we have previously observed in male gerbils interacting with 1-day-old foster young may have resulted from our studying responses to pups of either foster fathers or males that had never cohabited with females, rather than the pups' biological fathers.

In the Experiment 1, we compared directly responses to litters of newborn young of (a) virgin male foster fathers, (b) foster fathers that had fathered a litter other than the one they helped to rear, and (c) biological fathers. Our goal was to determine whether consanguinity or prior sexual experience affected the frequency with which male gerbils directed care-giving behaviors towards conspecific young. In Experiments 2 and 3, we further explored experiential effects on male gerbils' response to young, examining effects on paternal response of both cohabitation with a pregnant female (Experiment 2) and exposure to stimulation from pups (Experiment 3).

EXPERIMENT 1: RESPONSES TO PUPS OF BIOLOGICAL FATHERS, FOSTER FATHERS, AND VIRGIN MALES

We used the same unobtrusive measures of male gerbils' responses to pups that we have used in previous studies (Clark & Galef, 1999, 2000a, in press; Clark et al., 1998). First, on each day from the day of birth (Day 1 postpartum) to Day 20 postpartum, we determined the frequency with which male gerbils were (a) in contact with pups while their mates were either present in or away from the nest, and (b) crouched over the young in a ''nursing'' posture. Second, on Days 1 and 13 postpartum, we tested each male for his preference between pups and nest site. We have found that both the unobtrusive measures of male contact with pups and the test of relative preference of males for pups and nest site are sensitive to effects of endocrine and experiential manipulation of male gerbils (Clark, DeSousa, Vonk, & Galef, 1997; Clark & Galef, 1999, 2000a; Clark et al., 1998).

METHODS

Subjects

Thirty-three virgin male and 33 virgin female Mongolian gerbils selected at random from 60 litters born and reared in the vivarium of the McMaster University Psychology Department served as subjects. All subjects were fourth-generation descendants of breeding pairs acquired from Charles River (Brookfield, MA). An additional 11 proven male breeders from our colony served to impregnate 11 of the females.

We weaned all subjects at 32 days of age and, until the start of the experiment, maintained them in same-sex groups of 3 or 4 in opaque, polypropylene shoe-box cages ($35 \times 30 \times 15$ cm) closed with $^1/_2$-in. hardware cloth. All cages were housed in a single temperature- and humidity-controlled colony room, illuminated for 12 hr/day (light onset at 0500 hr). Throughout life, all subjects had ad libitum access to both tap water and pellets of Purina Rodent Laboratory Chow 5001 (Ralston Purina, Woodstock, Ontario).

Apparatus

During the experiment, each pair of adults and the young they were rearing were housed in shoe-box cages identical to those in which adults had been housed before weaning. At the appropriate time (see Procedure), we placed 30 g of cotton-batting nest material and a nest box constructed of clear Plexiglas (illustrated in Figure 1 and described in detail in Clark and Galef, 1999, 2000a) in the home cage of each pair. As can be seen in Figure 1, the nest box provided two identical compartments in which a nest could be built.

Procedure

Establishing Pairs and Composing Litters. When each of 22 of the male subjects reached 70 days of

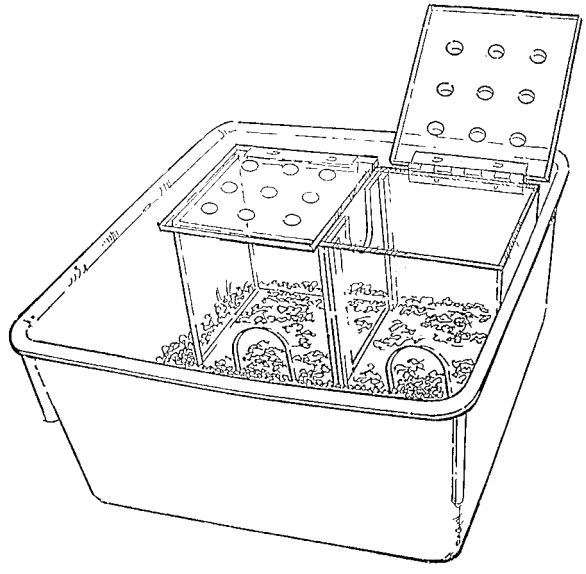

FIGURE 1 The apparatus used in experiments.

age, we paired him with a 60-day-old virgin female. The pair was monitored to determine when mating occurred with the expectation that a litter would be delivered 25 days after copulation. Ten days before the expected date of parturition, when a female was detectable pregnant, we placed a nest box and nesting material in the cage housing the pregnant female and her mate. We allowed the 11 males assigned to this Biological-Father condition to participate fully in rearing the litters that their mates delivered.

Ten days before the expected date of parturition, we removed the male from the cage of each of 11 pairs assigned to the Foster-Father condition and replaced each biological father with a male that had copulated with his mate on the same day as had the mate of the male he was to replace. Each foster father was left to help rear a litter that we culled immediately after testing on Day 1 (see Procedure) to the same size as one of the litters delivered by a female assigned to the Biological-Father condition.

Each of the remaining 11 females, those assigned to the Virgin-Male condition, were impregnated by 1 of 11 male breeders. Ten days before one of these females was due to deliver, we removed the breeder male from her cage and replaced him with a virgin male 90 to 100 days of age.

As with litters assigned to the Foster-Father condition, after testing on Day 1, we culled each litter assigned to the Virgin-Male condition to the same size as one of the litters being reared by subjects assigned to the Biological-Father condition.

To prevent aggression between females and unfamiliar males, when we introduced an unfamiliar male into a female's cage (Foster-Father and Virgin-Male conditions), we separated pair members for the first 24 hr with a hardware-cloth partition. To equate treatment of pairs assigned to the Biological-Father condition with that of males assigned to the other two conditions, 10 days before females in the Biological-Father condition were due to give birth, we separated them from their mates with a hardware-cloth partition for 24 hr.

Observation of Undisturbed Adults and Their Litters. Each day from the day of birth of a litter until its members were 20 days of age, an observer unaware of group assignment of litters recorded the behavior of the 33 male subjects and their mates. Starting 4 to 6 hr after light onset, once every 20 s for 15 min, the observer determined whether each adult in a cage was in physical contact with one or more pups and whether the male was huddled over the pups in a nursing posture. By recording separately those instances when a male was in contact with a litter while his mate was away from the nest, male contacts with the litter resulting from his attraction to his mate while she was in contact with the litter could be distinguished from male contacts with pups resulting from attraction of the litter itself (Clark et al., 1997).

Test of Preference Between Nest Site and Litter. Two hours after conclusion of unobtrusive observations on Days 1 and 13, each adult male subject was tested individually for his preference between pups and nest site. To perform this test, we first removed a pair of adults from their cage and placed them in a holding cage. We then moved all pups a pair was rearing from the compartment of the nest box that contained the nest to the other nest-box compartment. We waited 5 min for the pups to settle, then placed the adult male in the open area of the home cage facing away from both nest boxes.

During the next 30 min, an observer unaware of the group assignment of male subjects recorded the time that each male subject spent inside both nest-box compartments, one containing the nest and the other containing the pups.

At the end of the 30-min test period, the observer calculated a preference score for each male by dividing the number of min spent inside the nest-box compartment containing the pups by the total time spent in both nest-box compartments.

Data Analyses

We analyzed differences among groups using either one-way or between-within ANOVAs and Neuman-Keuls post-hoc tests. We used arcsine transformations to normalize variances of ratio data when these were heterogeneous.

RESULTS

The main results of Experiment 1 are presented in Table 1 and Figure 2.

Observation of Undisturbed Adults and Their Litters

Table 1 shows the percent of 20-s intervals on Day 1 and Days 2 to 20 during which male subjects were (a) in contact with pups, (b) in contact with pups while their mates were out of the nest (''baby-sat'' pups), and (c) in a brooding posture over the pups. As can be seen in Table 1, and as in our previous

Table 1. Parental Behaviors of Biological Fathers, Foster Fathers, and Virgin Males on Day 1 and Days 2 to 20 Postpartum

	Biological father ($n = 11$)	Foster father ($n = 11$)	Virgin male ($n = 11$)
Pup contact			
(Day 1)	23.0 ± 7.3	18.5 ± 7.9	21.1 ± 8.7
(Days 2 to 20)	69.5 ± 4.8	71.7 ± 4.9	74.2 ± 4.2
Huddling over pups	15.8 ± 3.2	12.6 ± 1.5	13.0 ± 2.2
"Baby sitting"[a]	71.4 ± 5.1	65.6 ± 3.7	66.3 ± 3.8

Note: Cell entries are means $\pm$ *SEM*s of the percentage of 20-s intervals that subjects engaged in each of the behaviors indicated.

[a]Percentage of 20-s intervals when dams were away from the nest when males were in contact with pups.

studies, all males were substantially less attentive to pups on Day 1 than on the following 19 days of observation, $F(1, 30) = 98.1$, $p < .0001$.

We failed to detect any effect of group assignment on males' response to pups either on Day 1, $F(2, 30) = .78$, n.s., or on subsequent days, $F(2, 30) = .24$, n.s. Biological fathers, foster fathers, and virgin males behaved indistinguishably on brooding and baby-sitting measures throughout the experiment, Fs$(2, 30) < .56$, n.s.

Test of Preference Between Nest Site and Litter

Figure 2 shows the results of the tests of males' preferences between pups and nest site carried out on Days 1 and 13 postpartum. A between-groups, repeated measure ANOVA provided no evidence of effects on males' preference for pups of either group assignment, $F(2, 30) = .43$, n.s., or pup age at testing, $F(2, 30) = .40$, n.s. We also failed to find a significant interaction between group assignment and pup age at testing, $F(2, 30) = .24$, n.s.

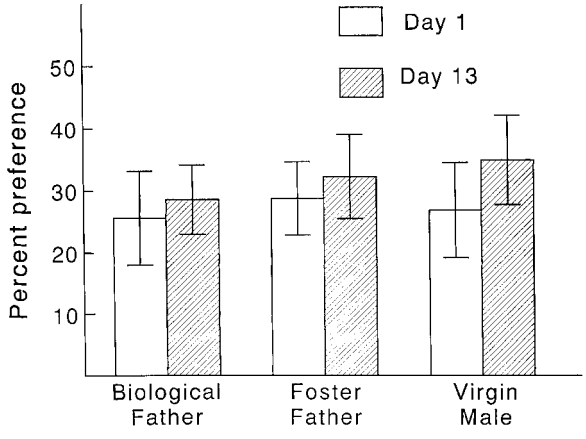

FIGURE 2 Mean amount of time (as a percentage of time in both nest-box compartments) that biological fathers, foster fathers, and virgin males spent in the nest-box compartment containing the pups. Error bars indicate *SEM*s.

DISCUSSION

Taken together, the results of the present experiment suggest that, as has been reported in several other rodent species (Brown, 1993), levels of parental responsiveness exhibited by male Mongolian gerbils to conspecific pups, both on the day of birth of a litter and throughout the preweaning period, do not vary as a function either of males' previous sexual experience or relatedness to pups.

EXPERIMENT 2: EFFECTS OF EXPOSURE TO PREGNANT FEMALES ON MALES' RESPONSES TO NEONATES

It might be argued that the failure in Experiment 1 to find a difference in responses to the young of virgin male foster fathers, sexually experienced foster fathers, and natural fathers either on the day of pup birth when males were relatively unresponsive to pups or on the following 19 days of male exposure to pups when males were quite parental reflected the 10 days of experience all males in Experiment 1 had cohabiting with a pregnant female whose litter they subsequently helped to rear. Elwood's (1977, 1980) finding that contact with a pregnant female inhibits infanticide in male Mongolian gerbils is consistent with such a hypothesis. However, the absence of infanticidal behavior in our gerbils and its frequency of occurrence in males in Elwood's studies make it difficult to know how to relate the two sets of experiments.

In Experiment 2, we examined directly effects of varying periods of cohabitation with a pregnant

female on responses of virgin male gerbils to conspecific neonates.

METHODS

Subjects

Thirty-six 100- to 120-day old virgin male and 36 virgin female Mongolian gerbils reared in the vivarium of the McMaster University Psychology Department, as described in Experiment 1, served as subjects.

Procedure

When the 36 female subjects were 30 days old, we paired 30 of them with a sexually proven male from our colony and paired 6 with mature (100- to 120-day-old) virgin males, and monitored all pairs to determine when mating occurred. Two days before a female was due to deliver, we placed a nest box (see Figure 1) and 30 g of nesting material in her cage.

Either 2 to 4 ($n = 8$), 5 to 7 ($n = 13$), or 8 to 10 ($n = 9$) days before a female gave birth, we placed 1 of the 30 virgin male subjects in her cage. As in Experiment 1, to eliminate aggressive interactions between newly formed pairs, for the first 24 hr that pair members shared a cage, we separated them with a hardware-cloth partition.

To provide a baseline of parental response by biological fathers, we paired each of the remaining 6 females with a mature virgin male and then left the pair undisturbed. Each male in this baseline group was exposed to a pregnant female for the entire 25 days of her pregnancy. On the day of birth of a litter, before a recently parturient female entered postpartum estrous, we tested each male for his preference between pups and nest box using the procedure described in Experiment 1.

RESULTS

The main result of Experiment 2 is presented in Figure 3, which shows the mean time that males spent in the nest-box compartment containing the pups as a percentage of the total time males spent in both nest-box compartments. As can be seen in Figure 3, the relative preference of males for pups and nests was significantly affected by the number of days that males spent with a pregnant female before delivery of her litter, $F(3, 35) = 5.32$, $p < .01$. Neuman-Keuls post hoc tests showed that (a) virgin males residing with pregnant females for 8 to 10 days before parturition

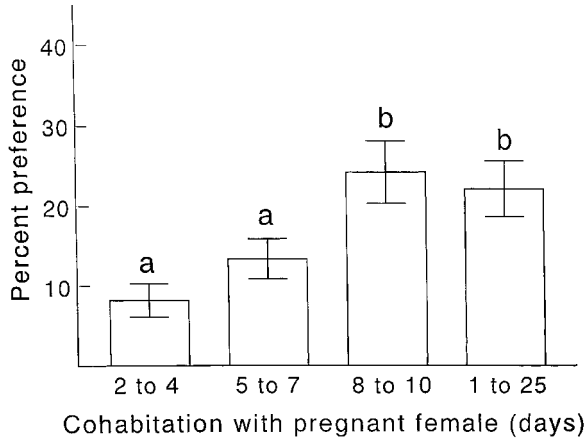

FIGURE 3 Mean amount of time (as a percentage of time in both nest-box compartments) that virgin males that had been exposed to pregnant females for varying lengths of time spent in the nest-box compartment containing pups. Error bars indicate *SEM*s. Histograms with different superscripts differ statistically ($p < .05$).

spent a significantly greater percent of time with pups than did males cohabiting with pregnant females for either 2 to 4 ($p < .01$) or 5 to 7 days ($p < .05$), and (b) there was no difference between the responses of males that had fathered a litter, lived with their pregnant mother for 25 days before testing, and were tested with their biological offspring and the responses of virgin males that had lived with a pregnant dam for only 8 to 10 days before being tested with unrelated young.

DISCUSSION

The present data are consistent with the hypothesis that exposure of a male gerbil to a pregnant female affects his response to her pups on the day of their birth. Virgin males exposed to a pregnant female for less than a week spent relatively less time with pups than did virgin males that had received more than a week of exposure to a pregnant dam. A week's exposure to a pregnant female was sufficient to produce levels of parental response in foster males similar to those seen in natural fathers that mated with females, remained with them throughout pregnancy, and interacted with their own offspring. Soroker and Terkel (1988) found, similarly, that exposing a male house mouse (*Mus musculus*) to cues from a pregnant conspecific female both inhibits infanticide and induces parental response in the male. The present finding, like that of Soroker and Terkel's, may be related to the demonstration in male California mice

(*Peromyscus californicus*) that exposing a male to either a postpartum female or her feces maintains the male's paternal response to her pups (Gubernick & Alberts, 1989).

EXPERIMENT 3: EFFECTS OF HUDDLING OVER PUPS ON MALES' RESPONSES TO 13-DAY-OLD PUPS

In our previous observations of the behavior of foster fathers helping to rear litters (Clark & Galef, 1999, 2000a; Clark, DeSousa, Vonk, & Galef, 1997; Clark et al., 1998), males responded to pups in one of two rather different ways: Either the males crouched over the young, assuming a posture much like that of a nursing dam, or males simply stayed in the nest in lateral contact with the young. Obviously, when huddled over pups, males received more tactile and thermal stimulation from young than when in the nest and in lateral contact with one or more pups.

In both virgin male and virgin female Norway rats, parental behavior can be induced by exposure to pups (Cosnier & Couturier, 1966; Fleming & Rosenblatt, 1974; Rosenblatt, 1967), particularly by tactile contact with them (Stern, 1983, 1996; Terkel & Rosenblatt, 1971). In the present experiment, we examined effects of crouching over young on males' subsequent response to young. We took advantage of our unpublished observations that (a) huddling over pups by males is largely restricted to the 15 to 20% of the day (Clark et al., 1998) when the female is away from the nest; (b) when males are alone with pups *and* pups are in the nest, males spend most of the time crouched over the young in a nursing posture; and (c) males infrequently crouch over pups when pups are outside the nest, even when the dam is absent.

METHODS

Subjects

Forty-eight litters of pups and their natural parents served as subjects.

Apparatus

The apparatus was that used in Experiments 1 and 2.

Procedure

Each family group was assigned to one of four groups that were treated identically, except for manipulations for 15 min each day from Days 2 to 12 postpartum. On each of these 11 days, litters assigned to one control condition were left undisturbed except for their removal from and immediate return to the nest. Pups in litters assigned to a second control condition were removed from their home cages, placed in an empty cage for 15 min, and then returned to their home cage.

In each of two experimental conditions, we removed dams from their home cages for 15 min, leaving fathers alone with their pups. Pups were either left in the nest, in which case we expected fathers to crouch over them in a nursing posture, or were placed in the empty compartment of the nest box, in which case we expected fathers to visit pups, but not to crouch over them. During each 15-min period when males assigned to the two experimental conditions were alone with pups, an observer recorded once every 20 s whether each male was crouched over the young in a nursing posture.

On Day 13, we tested fathers for their preferences between nest site and pups using the procedure described in Experiment 1.

RESULTS AND DISCUSSION

As expected, fathers left alone in a cage with young that had been displaced from their nest rarely crouched over the displaced pups ($11.6 \pm 3.7\%$ of observation periods) whereas fathers whose pups remained in the nest site frequently crouched over them ($64.2 \pm 5.1\%$ of observation periods). Males with both their mate and pups in the nest site crouched over pups on only $19.7 \pm 3.2\%$ of observations, $F(2, 32) = 47.94$, $p < .0001$.

Neuman-Keuls post hoc tests revealed that males alone in a cage with their pups in the nest crouched over pups significantly more frequently than did males assigned to the control group or to the other experimental group ($ps < .001$). The behavior of males in the latter two groups did not differ from one another. Of course, males in the control condition in which pups were removed from the home cage for 15 min/day could not crouch over them during the 15 min that the pups were absent.

Figure 4 shows the results of the test on Day 13 of males' preferences between pups and nest site. As can be seen in the figure, males that spent an additional 15 min/day in circumstances conducive to huddling over pups spent significantly more time with pups during testing than did males assigned to the other three conditions in which they did not have opportunity for extended huddling over pups, $F(3, 42) = 5.34$, $p < .01$. A Neuman-Keuls test revealed that males that

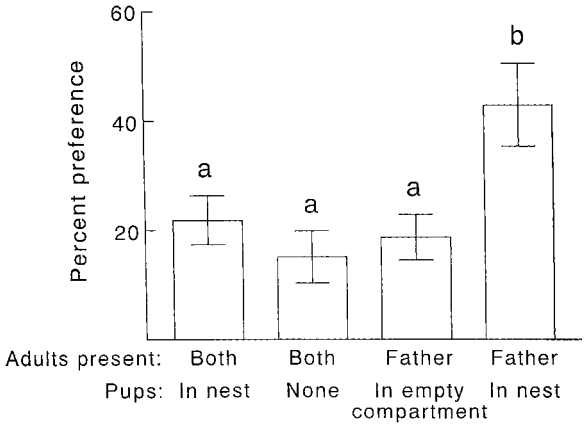

FIGURE 4 Mean amount of time (as a percentage of time in both nest-box compartments) that males in Experiment 3 spent in the nest-box compartment containing pups. Error bars indicate *SEM*s. Histograms with different superscripts differ statistically ($p < .05$).

had been exposed to pups in the nest with their dam absent spent a significantly greater percent of the test period with pups than did males assigned to each of the other three groups ($ps < .05$), which did not differ from one another. The results are consistent with the hypothesis that stimulation male gerbils receive from conspecific young while huddled over them enhances their responsiveness to pups.

GENERAL DISCUSSION

Experiment 1 showed that results of previous studies of responses to conspecific young of male gerbil foster fathers, either virgin or previously mated, can be generalized to natural fathers. In particular, the relatively low levels of response by males to day-old young that we reported previously proved to be restricted neither to foster fathers nor to sexually inexperienced males. Virgin male gerbils that could not possibly have been biological fathers of young they encountered and natural fathers that were closely related to young they helped rear did not differ in their response to conspecific young. Neither consanguinity nor possibility of paternity, factors that would influence the contribution of care of young to a male's direct fitness and might, therefore, be expected to affect his response to conspecific young (e.g., Davies, 1992; Elwood & Ostermeyer, 1984), had little or no impact on males' behavior.

Results of Experiments 2 and 3 showed that, unlike consanguinity and sexual experience, both exposure to pregnant dams and stimulation received as a result of intimate contact with pups were important modulators of male gerbils' responses to young. If, as we have previously proposed (Clark & Galef, 1999, 2000b; Clark et al., 1997), male gerbils increase their inclusive fitness (i.e., the total contribution of their genes to the next generation) by assisting in the rearing of nondescendant relatives, then facilitation of males' responsiveness to pups by exposure to cues from pregnant females and their young, even when the young are not the offspring of the exposed male, might be fitness enhancing. If so, the evolution of hormonal or neuronal mechanisms that would lead to positive response to pups by males that could not be biological fathers of pups they encountered might be anticipated.

Brown, Murdoch, Murphy, and Moger (1995) reported that the hormonal milieu of male Mongolian gerbils living with pregnant females differs from that of males living alone. In general, in the weeks following parturition, male Mongolian gerbils exposed to dams throughout their pregnancy and to dams and pups after parturition show elevated serum concentrations of prolactin and depressed serum concentrations of testosterone relative to males housed in isolation.

We reported previously that (a) castrated male gerbils are substantially more parental towards day-old young than are males with normal plasma concentrations of testosterone (Clark & Galef, 1999), and (b) male gerbils with naturally lower circulating levels of testosterone are more parental than are males with naturally higher circulating levels of testosterone (Clark et al., 1998). Apparently, testosterone titers of male gerbils are reduced by exposure to pregnant females and their young (Brown et al., 1995), testosterone inhibits males' response to pups (Clark & Galef, 1999; Clark et al., 1998), and increased exposure of male gerbils to either pregnant females or stimuli from pups enhances males' responses to young (Experiments 2 and 3 discussed earlier). Male helpers can reduce the cost to female gerbils of rearing litters (Clark et al., 1997). Taken together, these results are consistent with the hypothesis that exposure to stimuli from a pregnant female or her pups can reduce a male's circulating levels of testosterone, thus increasing his responsiveness to young.

In natural environments, male Mongolian gerbils in their first year often overwinter in their natal burrow with their dam, and she continues to be reproductively active (Gromov, 1981). Lowering of testosterone levels of a young male gerbil as a result of his exposure to a pregnant female and her offspring could, therefore, increase a male's inclusive fitness by increasing his willingness to invest in collateral kin.

NOTES

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