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Age-Related Changes in Paternal Responses of Gerbils Parallel Changes in Their Testosterone Concentrations

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ABSTRACT: Results of previous studies in our laboratory have shown that testosterone (T) inhibits parental response in adult male Mongolian gerbils. Here, we examined developmental changes in parental responses of male gerbils before, during, and after a naturally occurring surge in T that peaks on Day 75 postpartum. On the hypothesis that T inhibits parental response in male gerbils, we predicted that (a) 75-day-old male gerbils would be less responsive to neonates than would either younger or older male gerbils, and (b) young male gerbils whose T titers were rising as the litters that they were helping to rear matured would show a decrease over days in parental effort relative to older male gerbils whose T titers were falling as the litters that they were helping to rear matured. Both predictions were confirmed, providing evidence consistent with the view that naturally occurring, developmental changes in circulating concentrations of T play a role in age-related changes in the level of parental response of male Mongolian gerbils. © 2001 John Wiley & Sons, Inc. *Dev Psychobiol* 39: 179–187, 2001

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Male Mongolian gerbils (*Meriones unguiculatus*) housed with a female and young under laboratory conditions share parental duties with their mates, licking, huddling over, and retrieving pups (Elwood, 1975). Although all sexually experienced male gerbils become paternal (Elwood, 1979), males vary considerably in their response to conspecific young (Clark, DeSousa, Vonk, & Galef, 1997; Waring & Perper, 1980).

Previous studies have provided evidence that, as in birds (e.g., Hegner & Wingfield, 1987; Oring, Fivizzani, & El Halawani, 1989; Raouf, Parker,

Ketterson, Nolan, & Ziegenfus, 1997; Saino & Moller, 1995), elevated concentrations of testosterone (T) depress parental effort in adult male Mongolian gerbils. Castrated adult male gerbils are more attentive to conspecific young than are intact adult males, and placing Silastic capsules that restore T concentration levels of castrated males depresses their tendency to interact with young (Clark & Galef, 1999).

Naturally occurring variation in circulating concentrations levels of T also affect parental responsiveness of male gerbils; adult male gerbils that were gestated in intrauterine positions between male fetuses (2M males) have higher circulating concentrations of T in adulthood than do those that matured in intrauterine positions between female fetuses (2F males; Clark, vom Saal, & Galef, 1992), and 2M males are less responsive to young than are 2F males (Clark et al., 1997; Clark, Vonk, & Galef, 1998).

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EXPERIMENT 1

As can be seen in Figure 1 which is adapted from Probst (1987, Fig. 1), during development, mean circulating concentrations of T in male gerbils range from .3 to 4.2 ng/ml, peaking when males are roughly 75 days of age, an age at which they could be parents (Male gerbils in our laboratory have been seen mating when only 46 days old and have successfully impregnated females at 60 days of age. More than 90% of males are potent before reaching 80 days of age.)

In the present experiments, we took advantage of developmental fluctuation in concentration of T to further explore the relationship between naturally occurring variation in T levels and paternal responsiveness in gerbils. We made two predictions on the hypothesis that T inhibits response of male gerbils to conspecific young: first, that male gerbils of an age when they were experiencing peak concentrations of T should be less responsive to young than either older or younger male gerbils, and second, that there should be an interaction between the age of males at the time that they initiate care of a litter and the direction of change over days in their response to maturing young. Relative to males more than 75 days of age (that are experiencing declining T titers over days), males less than 75 days of age (that are experiencing rising T titers over days) should show a decrease in their response to growing young.

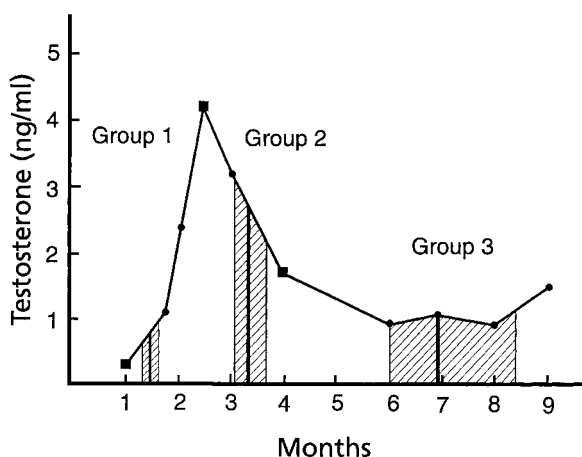


FIGURE 1 Square points indicating serum testosterone concentrations of male gerbils at various ages were taken from Probst's (1987) text; round points were read from Figure 1 of Probst (1987). Stippled areas indicate range of ages of males assigned to Group 1 (mean age = 41.8 days), Group 2 (mean age = 98.4 days), and Group 3 (mean age = 208.3 days) on the day of birth of the litter that each helped rear. The vertical line within each stippled area indicates the mean age of males in a group on the day of testing.

We used several unobtrusive measures of male gerbils' response to pups previously found to be sensitive to naturally occurring variation in circulating concentrations of T (Clark et al., 1997; Clark & Galef, 1999; Clark et al., 1998). First, we determined the time that males spent together with pups when their mate was both present in and away from the nest. Although time in contact with pups is not necessarily a measure of parental behavior (Males might, for example, be motivated to remain in the nest or in contact with their mates and only inadvertently contact young [Clark et al., 1998].), pup contact has been used previously either alone (e.g., Grotta & Ader, 1969; Storey & Snow, 1987; Wynne-Edwards, 1995) or in combination with more direct measures of parenting (Gubernick & Alberts, 1987; Solomon, 1993) to measure parental effort in several rodent species.

We also used two more direct measures of parental behavior: the frequency with which males huddled over pups while in a nursing posture ("brooded" the young) and the frequency with which males licked pups.

Method

Subjects. Fifty-two virgin male Mongolian gerbils and 52 female gerbils that were in postpartum estrous after delivering their first litters, all born and reared in the vivarium of the McMaster University Psychology Department, served as subjects. All 104 subjects were descendants of breeding stock acquired from Charles River Canada (St. Constant, Quebec).

When each male subject was 32 days old, we assigned him to one of three groups that varied in the age at which group members were (a) paired with subject females and (b) tested for parental responsiveness.

Controlling for Seasonal Effects. We have previously reported seasonal differences in reproductive behavior of Mongolian gerbils maintained in 'constant' laboratory conditions (Clark, Spencer, & Galef, 1986). If we had started all subjects in the experiment on the same date and tested them at different ages, there would have been systematic differences among the groups not only in age at testing but also in the month of the year when testing occurred. Conversely, if all subjects had been tested in the same month, there would have been systematic differences among the groups not only in age at testing but also in the month of the year at birth.

To insure that differences in behavior of subjects assigned to the three groups in the present experiment

reflected differences in their ages rather than differences in the months when they were born or tested, we assigned subjects to groups so that half the subjects in each group were born in the same month and half were tested in the same month.

Apparatus. We housed all male subjects, their mates, and the litters that they were rearing in opaque, polypropylene cages measuring $35 \times 30 \times 15$ cm. The top of each cage was closed with 1/2 in. (1.3 cm) hardware cloth, and its floor was covered with a layer of wood-chip bedding.

At an appropriate time (see Procedure), we placed a nest box measuring $28 \times 12.7 \times 12.7$ cm within the home cage of each mated pair. The nest box, constructed of transparent Plexiglas, was divided into two identical compartments separated by a 12.7 cm square, transparent Plexiglas partition, and had two entrance holes (5 cm in diameter) that permitted subjects direct access from the remaining 23.3×30 cm open area of each cage into the nest box compartments (Fig. 2). A third 5-cm diameter opening cut at the top of the partition that divided the nest box into separate compartments permitted adult, but not juvenile, gerbils to pass directly from one compartment of the nest box to the other. Hinged lids of transparent Plexiglas allowed an experimenter access to each compartment, and holes drilled through these lids provided ventilation within the nest box. When we placed a nest box with a female, we also provided her with 5 g of cotton batting to use as nesting material.

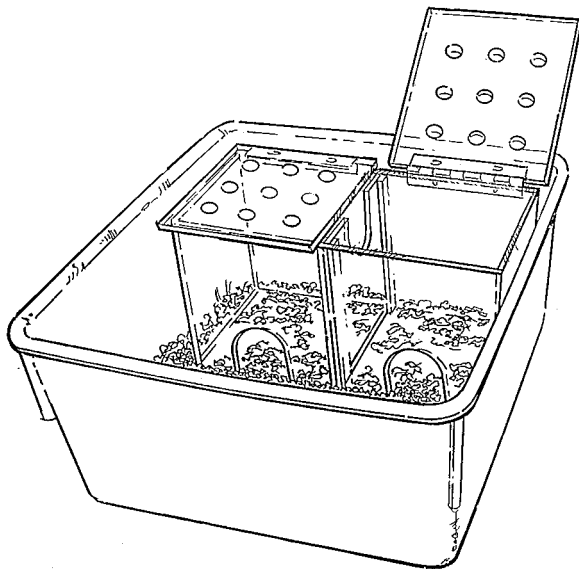


FIGURE 2 Multichambered cages used in the experiment are shown.

Procedure

Treatment of subjects: Group 1. When the first litter born to each of 20 females was 32 days old, we removed all litter members except 1 male (Removed pups were used as subjects in other studies.), placed a nest box and nest material in the open area of the cage, and left the single male with his dam. These dams had been reimpregnated during the postpartum estrous that followed the birth of their first litters, and each female delivered her second litter 40 to 44 days after the birth of her first litter (The normal gestation period for Mongolian gerbils is 25 to 26 days, but lactating females can delay implantation of the litter conceived in postpartum estrous [Norris & Adams, 1981], and older males often are somewhat slower than young ones to impregnate females [author's observation], so there can be considerable variance between the time a male is placed with a female and her delivery.) Male subjects were 41.8 ± 0.6 (mean ± 1 SEM) days of age when their dams delivered their second litters.

To control for possible effects of variation in size or sex composition of litters on the behavior of subjects (Clark & Galef, 1990; Elwood & Broom, 1978), on the day of a female's parturition, immediately after the unobtrusive measure of male parental behavior on Day 1 (discussed later), we replaced her second litter with 4 male and 4 female foster pups taken from a female or females that had given birth during the 24 h immediately preceding delivery by the subject female.

Treatment of subjects: Group 2. We weaned male subjects assigned to Group 2 ($n = 20$) when they were 32 days of age and placed them in groups of 3 or 4. When each male was 70 days old, we paired him with a female in postpartum estrous with the expectation that females would produce their second litters when subject males were 95 to 110 days old.

To prevent aggression between animals unfamiliar to one another, when we first introduced males into the cages of females, we separated pair members with a hardware cloth partition. Four hours later, we removed the partition, allowing males to come into contact with their partners.

We placed a nest box in the cage of each pair when the female was visibly pregnant, late in the 2nd week of her gestation. Male subjects were, on average, 98.4 ± 3.6 days of age when their female consorts delivered their second litters.

As in Group 1, on the day of birth of a female's second litter, we replaced her natural litter with 4 male and 4 female foster pups taken from a female or females that had given birth during the 24 hr immediately preceding delivery by the subject female.

Treatment of subjects: Group 3. We treated subjects in Group 3 ($n=12$) exactly as we treated subjects in Group 2 except that we paired each male assigned to Group 3 with a female in postpartum estrous when the male was 150 days old with the expectation that females would deliver their second litters when the males were 175 or more days of age. Male subjects were 208.3 ± 8.1 days of age when their dams delivered their second litters.

Unobtrusive observations of male parental behavior. On each day from Day 1 to Day 20 postpartum, 4 hr after light onset, an experimenter unaware of the purpose of the experiment observed the 52 subject males and their mates. The observer recorded once each 20 s, for 15 consecutive min, whether each adult was in physical contact with one or more members of the litter in its cage. The experimenter also recorded at each inspection whether males were huddled over pups and whether they were licking pups.

By examining separately those instances when a male was in contact with a litter while its mate was away from the nest, it was possible to distinguish male contacts with the litter resulting from male attraction to the litter from male contact with a litter that resulted from a male's attraction to his mate while she was in contact with the litter (Clark et al., 1997).

Tests of pup preference. Two hours after the end of the 15-min period of unobtrusive observation, on the day pups in each litter assigned to Groups 1 and 2 were 1 and 13 days old, we tested them for their preferences between pups and nest site. To avoid confounds due to repeated testing of the same animals, we randomly selected half of the males in each group for testing on Day 1 and tested the remainder on Day 13. To perform a test, we first removed both adults from their home cage and placed them in a holding cage. We then moved the 8 foster pups a pair was rearing from whichever nest-box compartment contained the nest, and placed the entire litter on the opposite side of the partition dividing the nest box. We then waited for 5 min before placing the male in the open area of its home cage, facing away from the nest box. During the next 30 min, an observer recorded the time the male spent in the nest-box compartment where the pups were now located and in the nest-box compartment containing the nest.

Each male was awarded a preference score calculated by dividing the number of min that it spent in the nest-box compartment with the pups by the total time that it spent in both nest-box compartments.

We did not test males in Group 3 for their preference between pups and nest site. Males assigned to Group 3 were at an age when their T titers would be expected to remain constant as the pups that they were helping to rear matured. Consequently, any changes in the responsiveness to pups of males in Group 3 would reflect changes only in the pups themselves rather than changes in the internal state of the males, and we were interested here in effects on the parental responsiveness of males of changes in their testosterone titers.

Results

A 3×2 (Ages \times Assignments) ANOVA revealed no effect of month of birth or testing on any measure, $F_s(1, 46) < 1.94$, n.s., a significant effect of age of male subjects at observation and testing on all measures, $F_s(2, 46) > 5.63$, $ps < .007$, and no significant interactions between main effects, $F_s(2, 46) < 1.85$, n.s. Consequently, we combined data from subjects born in the same month and subjects tested in the same month in all subsequent analyses.

The main results of Experiment 1 are presented in Figures 3 and 4. Figure 3 shows the mean number of observation periods of a total of 900 (3 times/min \times 15 min \times 20 days) that (top panel) subject males and their mates were simultaneously in contact with pups, (middle panel) males huddled over pups while in a nursing posture, and (lower panel) males "baby-sat" pups (i.e., were in contact with pups while their mates were away from the nest).

As can be seen in Figure 3, there was a significant effect of group assignment on each of the three measures of parental response, one-way ANOVAs: $F_s(2, 49) > 5.37$, $ps < .01$. On all three measures, males assigned to Group 2 were significantly less responsive to pups than were males assigned to Groups 1 and 3, LSD tests: $ps < .05$, and males assigned to Groups 1 and 3 differed from one another only in percent time spent huddled over pups in a nursing posture, LSD test: $p < .01$.

On the hypothesis that changing levels of T affect male parental responsiveness, it also might be expected that there would be an interaction between the age at which males started to interact with newborn young and the change over time in measures of response to pups. As pups matured, males in Group 1 (whose T titers were increasing) should have shown decreasing levels of parental care relative to males in Group 2 (whose T titers were decreasing). In fact, an ANOVA examining the amount of time males in Groups 1 and 2 spent in contact with pups during Days 1 to 6 postpartum and Days 7 to 12 postpartum showed a significant effect of group, $F(1, 38) = 7.70$,

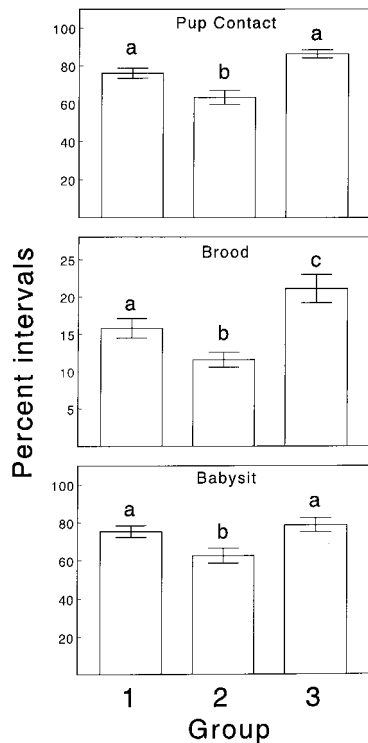


FIGURE 3 Mean percentage of 20-s intervals during 20 successive days of 15-min observations when male gerbils assigned to Groups 1, 2, and 3 were (upper panel) together with their mate and in contact with young, huddled over the young while in a nursing posture (middle panel), and in contact with young while their mate was away from the nest (“baby-sitting”) (lower panel). Vertical lines depict ± 1 SEM. Histograms with different superscripts differed significantly ($p < .05$).

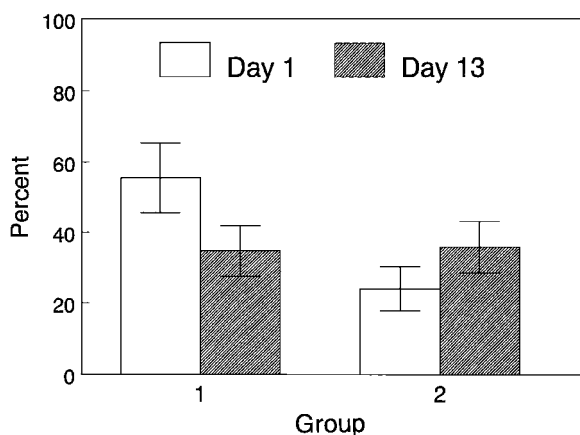


FIGURE 4 Mean percentage of time on Days 1 and 13 that males in Group 1 (increasing T titers) and Group 2 (decreasing T titers) were in either nest-box compartment that they were in the nest-box compartment containing the young. Vertical lines depict ± 1 SEM.

$p < .01$, but not age of pups, $F(1, 49) = .62$, n.s., and most importantly, a significant Group \times Age interaction, $F(2, 49) = 6.21$, $p < .02$, resulting from subjects in Group 1 showing an increase over days and subjects in Group 2 showing a decrease over days in frequency of pup contact. The same interaction was observed when data from Day 1 (when males in Group 1 were far more likely than those in Group 2 to be seen in contact with pups) were not included in the analysis and data from Day 13 were added to equate the number of days examined with those in the first analysis, $F(1, 38) = 8.52$, $p < .01$.

We found no reliable differences in the frequency with which males assigned to the various groups licked pups, $F(2, 49) = 1.06$, n.s. Licking of pups by males occurred most often when a male returned to the nest site after an excursion away from it (Clark, unpublished observations; Moore, Wong, Daum, & Leclair, 1997). Pup licking was, therefore, a better index of number of departures from the nest than of attention to young.

Figure 4 shows the results of preference tests of independent groups of male gerbils for pups on Days 1 and 13 of the experiment. Data from 3 males in Group 1 were lost when the males retrieved pups back to the original nest site, thus precluding measurement of a preference between nest site and pups.

There was a significant main effect on pup preference of age of subject males at the initiation of the experiment, but not of day of testing; 2×2 ANOVA, $F(1, 33) = 4.11$, $p < .05$; $F(1, 33) = \text{n.s.}$ Most important as a test of the hypothesis that changing concentrations of T affected male response to pups, there was a significant interaction between male's age at initiation of the experiment and day of testing, $F(1, 33) = 4.73$, $p < .04$. As can be seen in Figure 4, this interaction resulted from a tendency of subjects assigned to Group 1 to show a decrease and for subjects assigned to Group 2 to show an increase in preference for pups from Day 1 to Day 13.

Discussion

On the hypothesis that paternal responsiveness and T titers of male gerbils are inversely correlated, we had predicted, first, that male gerbils from 2 to 4 months of age (those with relatively high circulating concentrations of T) would show less responsiveness to conspecific young than either older or younger male gerbils (those with relatively low circulating concentrations of T), and second, that male gerbils less than 2 months of age (whose T titers were rising) would show a decrease in response to maturing young relative to male gerbils more than 3 months of age

(whose T titers were falling). Both predictions were confirmed. Males in Group 2, with relatively high circulating concentrations of T, spent less time with young and were less likely to huddle over them in a nursing posture than were males in either Group 1 or Group 3 that had relatively low circulating concentrations of T. Relative to males in Group 2 (that were experiencing a drop in circulating concentrations of T over the 13 days of the experiment when pups were relatively immobile), males in Group 1 (that were experiencing a rise in circulating levels of T) showed a decline in preference for young during preference tests and a decrease in time in contact with pups.

There are, of course, problems in interpreting the data of Experiment 1. Although subjects in Groups 2 and 3 were reared identically (except for the age at which they were tested), subjects in Group 1 were treated quite differently from those in Groups 2 and 3. For example, males in Group 1 had the opportunity to copulate with a female before testing and interacted with siblings rather than unrelated young. It is surely possible that these differences in treatment, rather than differences in plasma concentrations of T, were responsible for the observed differences in parental behavior observed in Groups 1 and 2 (Clark & Galef, 2000a; French, 1994; Ostermeyer & Elwood, 1984). Consequently, it cannot be determined whether differences between the behavior of subjects in Groups 1 and 2 reflected differences in their plasma T concentrations or differences in their maintenance conditions. In Experiment 2, we controlled for all such potential confounds and examined directly the relationship of age of male subjects on their responsiveness to pups.

EXPERIMENT 2

In Experiment 2, we measured the parental behavior of male gerbils of different ages that had been maintained identically before testing. We again used Probst's (1987) data to establish groups that differed in their circulating levels of T (see Table 1 and Fig. 5).

On the hypothesis that paternal responsiveness is suppressed by T, parental response would be expected (a) to decrease from Groups 1 to 3 when T levels were rising (Probst, 1987); (b) to increase from Groups 4 to 6 when T concentrations were falling (Probst, 1987); (c) to be greatest in Group 1, the group expected to have the lowest circulating concentrations of T (Probst, 1987); and (d) to be lowest in Group 4, the group expected to have the highest circulating concentrations of T (Probst, 1987).

Table 1. Number of Subjects Assigned to the Seven Groups in Experiment 2, Their Range of Ages at Pairing, and Mean Ages When Females Gave Birth

Group	n	Age at Pairing	Age at Birth of Litter
		Range (Days)	Mean (Days) (SEM)
1	13	32–36	39.6 (± 1.0)
1a	10	31–62	41.1 ($\pm .9$)
2	28	40–48	50.8 ($\pm .6$)
3	24	49–57	59.2 ($\pm .2$)
4	11	58–64	71.8 (± 1.1)
5	10	71–80	82.4 (± 1.3)
6	14	90–110	108.5 (± 4.2)

Method

Subjects. Subjects were 100 male gerbils selected from 98 litters born and reared in the vivarium of the Department of Psychology of McMaster University treated as were subjects assigned to Groups 2 and 3 of Experiment 1 except that (a) subjects were reared by dams that had not been impregnated during postpartum estrous, and (b) litters were weaned to same-sex groups of 3 or 4 siblings when 30 rather than 32 days of age.

When each male subject was 30 days old, we assigned him to one of six groups that varied in the age at which group members were placed with a pregnant female and tested for parental responsiveness. The number of males assigned to each of the six

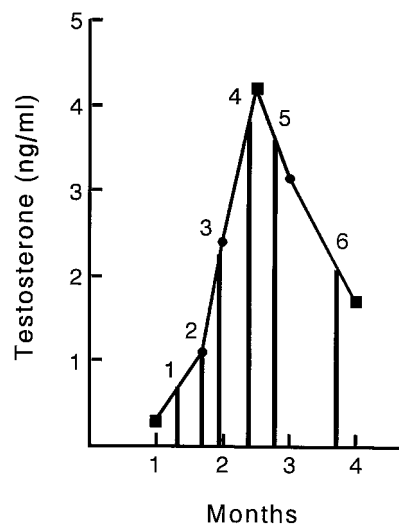


FIGURE 5 Square points indicate serum testosterone concentrations of male gerbils and were taken from Probst's (1987) text; round points were read from Figure 1 of Probst (1987). The vertical lines indicate the mean ages of males in Groups 1 to 6 on the day of testing.

groups, their range of ages when paired with females, and mean age (± 1 SEM) when females gave birth are shown in Table 1.

To determine the effects, if any, on parental responsiveness of the differences in treatment received by subjects in Groups 1 and 2 in Experiment 1, we examined 10 subjects from 10 additional litters (Group 1a). Subjects assigned to Group 1a were reared and maintained identically to subjects in Group 1 in Experiment 1 and were tested as were subjects in Groups 1 to 6 of the present experiment.

Apparatus. The apparatus was that used in Experiment 1.

Procedure. We paired each male subject with a female that was 15 to 22 days pregnant and used the methods employed in Experiment 1 to eliminate aggression when pairing unfamiliar animals.

To ensure that subjects did not differ in sexual experience at the time they were tested, we examined subjects' parental behavior only on the day on which the female with which they were paired gave birth. Female gerbils are not sexually receptive while pregnant and enter postpartum estrous roughly 24 hr following parturition.

On the day of birth of a litter, we first determined the percent of observation periods that each male spent in contact with the litter in his cage, and 1 hr later, tested him for his preference between nest and pups, as in Experiment 1.

Results and Discussion

We could not test 7 subjects (1 each from Groups 2 and 4, and 5 from Group 3) because the litters with which these subjects were to be tested were either partially cannibalized (by an unidentified parent) or unhealthy. An additional subject in Group 6 and 2 subjects in Group 1a did not receive scores on the preference test because each retrieved pups to the nest site.

The main results of Experiment 2 are presented in Figure 6, which shows the mean percentage of the 15-min observation period that males in Groups 1 to 6 were in contact with pups (upper panel) and the results of the choice test between pups and nest site on the pups' day of birth (lower panel). As can be seen in Figure 6, there was a significant effect of subject age on both frequency of pup contact, $F(5, 92)=8.10$, $p < .0001$, and preference for pups in the choice test, $F(5, 91)=3.32$, $p < .01$. Newman-Keul's post hoc tests revealed that, on both measures of pup contact, subjects in Group 1 (that had the lowest circulating

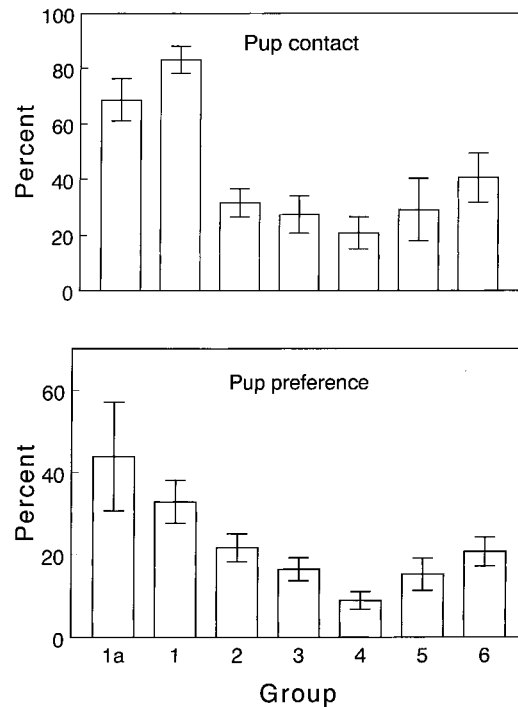


FIGURE 6 Upper panel: Mean percent (± 1 SEM) of a 15-min observation period on the day of birth of pups that males in Groups 1 to 6 and 1a were in contact with pups. Lower panel: Mean percent (± 1 SEM) of a 30-min observation period on the day of birth of pups that subject males in Groups 1a and 1 to 6 were in either nest-box compartment that they were in the nest-box compartment containing the young.

levels of T) were significantly more responsive than were subjects in any of the other five groups, and on both measures of parental responsiveness, subjects in Group 4 (that had the highest circulating levels of T) had the lowest average scores, an event relatively unlikely to occur by chance alone, although there does not seem to be a good statistical measure of the probability of such an outcome.

To further examine the prediction that parental behavior should decrease with increase in circulating levels of T and increase with decreasing levels of T, we looked at trends in parental behavior in Groups 1 to 3, when T titers were rising sharply, and Groups 4 to 6, when T titers were falling. On both measures of parental responsiveness, there was a significant downward linear trend to the data for Groups 1 to 3, $F_s(1, 612) > 7.92$, $ps < .01$. On the measure of preference between pups and nest site, there was a significant linear increase from Groups 4 to 6, $F(1, 31)=4.49$, $p < .04$, and on the measure of pup

contact, a marginal increase from Groups 4 to 6, $F(1, 32) = 2.66, p = .11$.

Comparison of the behavior of subjects in Groups 1 and 1a revealed no significant difference in either measure of parental responsiveness (Student's t tests: time in contact with pups $t(21) = 1.55$, n.s.; percent preference for pups, $t(19) = .89$, n.s., a result consistent with the hypothesis that the differences in parental response between subjects in Group 1 and subjects in Group 2 in Experiment 1 were the result of differences in their T titers, not differences in the conditions of their maintenance.

All of the results of Experiment 2 are thus consistent to varying degrees of statistical reliability, with each of the four predictions based on the hypothesis that developmental changes in T effect parental response in male gerbils described in the introduction to the present experiment.

GENERAL DISCUSSION

Immature male Mongolian gerbils, the subjects in the present experiments, like other immature rodents examined to date (Siberian hamsters: Gibber, Piontkewitz, & Terkel, 1984; voles: Roberts, Miller, Taymans, & Carter, 1998; rats: Mayer, Freeman, & Rosenblatt, 1979; Brunelli, Shindedecker, & Hofer, 1985; mice: Svare, Kinsley, Mann, & Broida, 1984), respond more parentally toward conspecific neonates than do sexually mature individuals. The present results are consistent with the hypothesis that naturally occurring developmental changes in circulating concentrations of T may play a role in such age-related changes in male responsiveness to young.

The present findings, although consistent with the hypothesis that changes in circulating concentrations of T cause changes in male gerbils' responses to young are, of course, correlational and cannot provide conclusive evidence of effects of T on paternal behavior. Circulating concentrations of hormones other than T (e.g., prolactin and oxytocin) can fluctuate with age (Meites, Steger, & Huang, 1980), and such changes in hormonal substrate could be responsible for the age-related changes in parental response that we observed. However, taken together with previous demonstrations that artificially induced changes in circulating level of T profoundly influence the response of male gerbils to conspecific young (Clark & Galef, 1999), the present results suggest that naturally occurring developmental changes in plasma concentration levels of T are responsible for at least some of the observed age-related variation in parental responsiveness of male Mongolian gerbils.

If the present results can be extrapolated to gerbils of greater ages than those studied here, one might expect to see an increase in parental behavior in male gerbils as they age and their production of T declines. Further, to the extent that the present results generalize across rodent species, one might expect to see low levels of T in males of biparental rodents, such as prairie voles (*Microtus ochrogaster*) and California mice (*Peromyscus californicus*), relative to closely related species in which females undertake most or all parental duties. In fact, published reports of T titers in adult male prairie voles (Bamshad, Novak, & de Vries, 1994) and California mice (Gubernick & Nelson, 1989) suggest that both have unusually low circulating levels of T, although such measures are more difficult to interpret in species in which T titers of males fluctuate markedly than in species that, like the Mongolian gerbil, have quite constant circulating levels of T (Probst, 1987).

NOTES

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REFERENCES

- Bamshad, M., Novak, M. A., & de Vries, G. A. (1994). Cohabitation alters vasopressor innervation and paternal behavior in Prairie voles (*Microtus ochrogaster*). *Physiology & Behavior*, 56, 751–758.
- Brunelli, S. A., Shindedecker, R. D., & Hofer, M. A. (1985). Development of maternal behaviors in prepubertal rats at three ages: Age-characteristic patterns of response. *Developmental Psychobiology*, 18, 309–326.
- Clark, M. M., DeSousa, D., Vonk, J., & Galef, B. G., Jr. (1997). Parenting and potency: Alternative routes to reproductive success in male Mongolian gerbils. *Animal Behaviour*, 54, 635–642.
- Clark, M. M., & Galef, B. G., Jr. (1990). Evidence of sex-biased postnatal maternal investment by Mongolian gerbils. *Animal Behaviour*, 39, 735–744.
- Clark, M. M., & Galef, B. G., Jr. (1999). A testosterone-mediated trade-off between parental and sexual effort in male Mongolian gerbils (*Meriones unguiculatus*). *Journal of Comparative Psychology*, 113, 388–395.
- Clark, M. M., & Galef, B. G., Jr. (2000a). Effects of experience on the parental response of male Mongolian gerbils. *Developmental Psychobiology*, 36, 177–185.
- Clark, M. M., Spencer, C. A., & Galef, B. G., Jr. (1986). Reproductive life history correlates of early and late

- sexual maturation in Mongolian gerbils (*Meriones unguiculatus*). *Animal Behaviour*, 34, 551–560.
- Clark, M. M., vom Saal, F. S., & Galef, B. G., Jr. (1992). Intrauterine position and testosterone levels of adult male gerbils are correlated. *Physiology & Behavior*, 51, 957–960.
- Clark, M. M., Vonk, J., & Galef, B. G., Jr. (1998). Intrauterine position, parenting, and nest site-attachment in male Mongolian gerbils. *Developmental Psychobiology*, 32, 177–181.
- Elwood, R. W. (1975). Paternal and maternal behaviour in the Mongolian gerbil. *Animal Behaviour*, 23, 766–772.
- Elwood, R. W. (1979). Maternal and paternal behavior of the Mongolian gerbil: A correlational study. *Behavioral and Neural Biology*, 25, 555–562.
- Elwood, R. W., & Broom, D. M. (1978). The influence of litter size and parental behavior on the growth of Mongolian gerbil pups. *Animal Behaviour*, 26, 438–454.
- French, J. A. (1994). Alloparents in the Mongolian gerbil: Impact on long-term independent reproduction. *Behavioral Ecology*, 5, 273–279.
- Gibber, J. R., Piontkewitz, Y., & Terkel, J. (1984). Response of male and female Siberian hamsters towards pups. *Behavioral and Neural Biology*, 42, 177–182.
- Grota, L. J., & Ader, R. (1969). Continuous recording of maternal behaviour in *Rattus norvegicus*. *Animal Behaviour*, 17, 722–729.
- Gubernick, D., & Alberts, J. R. (1987). The biparental care system of the California mouse, *Peromyscus californicus*. *Journal of Comparative Psychology*, 107, 169–177.
- Gubernick, D. J., & Nelson, R. J. (1989). Prolactin and paternal behavior in the biparental California mouse, *Peromyscus californicus*. *Hormones and Behavior*, 23, 203–210.
- Hegner, R. E., & Wingfield, J. C. (1987). Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk*, 104, 462–469.
- Mayer, A. D., Freeman, N. C. G., & Rosenblatt, J. S. (1979). Ontogeny of maternal behavior in the laboratory rat: Factors underlying changes in responsiveness from 30 to 90 days. *Developmental Psychobiology*, 12, 425–439.
- Meites, J., Steger, R. W., & Huang, H. H. H. (1980). Relation of the neuroendocrine system to the reproductive decline in aging rats and human subjects. *Federation Proceedings*, 39, 3168–3172.
- Moore, C. L., Wong, L., Daum, M. C., & Leclair, O. U. (1997). Mother–infant interactions in two strains of rats: Implications for dissecting and function of a maternal pattern. *Developmental Psychobiology*, 30, 301–312.
- Norris, M. L., & Adams, C. E. (1981). Mating postpartum and length of gestation in the Mongolian gerbil (*Meriones unguiculatus*). *Laboratory Animals*, 15, 189–191.
- Oring, L. W., Fivizzani, A. J., & El Halawani, M. E. (1989). Testosterone induced inhibition of incubation in the spotted sandpiper (*Actitis macularia*). *Hormones and Behavior*, 23, 412–423.
- Ostermeyer, M. C., & Elwood, R. W. (1984). Helpers(?) at the nest in the Mongolian gerbil, *Meriones unguiculatus*. *Behaviour*, 91, 61–77.
- Probst, B. (1987). Developmental changes in the pituitary–gonadal axis in male Mongolian gerbils from birth to adulthood. *Experimental and Clinical Endocrinology*, 90, 157–166.
- Raouf, S. A., Parker, P. G., Ketterson, E. D., Nolan, V., Jr., & Ziegenfuss, C. (1997). Testosterone affects reproductive success by influencing extra-pair fertilizations in male dark-eye juncos (*Aves: Junco hyemalis*). *Proceedings of the Royal Society, London (Series B)*, 264, 1–5.
- Roberts, R. L., Miller, A. K., Taymans, S. E., & Carter, C. S. (1998). Role of social and endocrine factors in alloparental behavior of prairie voles (*Microtus ochrogaster*). *Canadian Journal of Zoology*, 76, 1862–1868.
- Saino, N., & Moller, A. P. (1995). Testosterone induced depression of male parental behavior in the barn swallow: Female compensation and effects on seasonal fitness. *Behavioral Ecology and Sociobiology*, 36, 151–157.
- Solomon, N. G. (1993). Comparison of parental behavior in male and female prairie voles (*Microtus ochrogaster*). *Canadian Journal of Zoology*, 71, 434–437.
- Storey, A. E., & Snow, D. T. (1987). Male identity and enclosure size affect paternal attendance of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, 35, 411–419.
- Svare, B., Kinsley, C. H., Mann, M. A., & Broida, J. (1984). Infanticide: Accounting for genetic variation in mice. *Physiology & Behavior*, 33, 137–152.
- Waring, A., & Perper, T. (1980). Parental behaviour in Mongolian gerbils (*Meriones unguiculatus*): II. Parental interactions. *Animal Behaviour*, 28, 331–340.
- Wynne-Edwards, K. E. (1995). Biparental care in the Djungarian but not Siberian dwarf hamsters (*Phodopus*). *Animal Behaviour*, 50, 1571–1585.