Journal of Comparative Psychology
1999, Vol. 113, No. 4, 388–395

0735-7036/99/$3.00

A Testosterone-Mediated Trade-Off Between Parental and Sexual Effort in Male Mongolian Gerbils (*Meriones unguiculatus*)

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Effects of testosterone (T) on parental behavior of male Mongolian gerbils (*Meriones unguiculatus*) were examined. After undergoing gonadectomy, castrated males were implanted with empty capsules or capsules containing T; sham-operated males were implanted with empty Silastic capsules. Subsequently, each male was paired with a pregnant female, and after delivery, families were observed 15 min/day for 20 days. Gonadectomized males without T spent more time in contact with, huddling over, and licking pups than did either sham-operated males or gonadectomized males with T. When given a choice between nest sites and displaced pups, females and males with low T preferred pups, whereas intact males and castrated males with T preferred nest sites. The findings are consistent with E. D. Ketterson and V. Nolan's (1994) hypothesis implicating T in mediating trade-offs between parental and sexual effort.

In the laboratory, male Mongolian gerbils (*Meriones unguiculatus*) generally share parental duties with their mates. Like females of their species, male Mongolian gerbils huddle over, lick, and retrieve pups (Elwood, 1975).

Although all male gerbils engage in some parental behavior, they vary considerably in the frequency with which they interact with young. This variation in parental behavior of males is correlated with the intrauterine positions (IUPs) that males occupied as fetuses and their circulating levels of testosterone (T) both in infancy and in adulthood. Males gestated in IUPs between two female fetuses (2F males) have lower circulating levels of T throughout life and as adults spend more time with pups than do males gestated in IUPs between two male fetuses (2M males; Clark, DeSousa, Vonk, & Galef, 1997; Clark, vom Saal, & Galef, 1992).

Adult circulating levels of T also have marked effects on the sexual behavior of male Mongolian gerbils. Like gonadectomized male rats (Baum, 1993), gonadectomized male gerbils engage in little sexual behavior, whereas both intact males and males gonadectomized as adults and given Silastic implants of T are sexually active (Ulibarri & Yahr, 1996; Yahr, Newman, & Stephens, 1979). As one also would expect on the basis of the hypothesis that high circulating levels of T in adulthood are correlated with enhanced sexual behavior in male gerbils, 2M male gerbils are more sexually active than 2F male gerbils (Clark, Tucker, & Galef, 1992).

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This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada.

We thank Paul Ramos, Jessica Stevens, Jennifer Vonk, and Elaine Whiskin for technical assistance.

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Ketterson and Nolan (1994, in press) proposed that circulating levels of plasma androgens mediate a trade-off between sexual and parental effort in male birds. In many avian species, artificially elevated levels of T increase sexual effort of males but reduce their care of eggs and young (e.g., Hegner & Wingfield, 1987; Oring, Fivizzani, & El Halawani, 1989; Saino & Moller, 1995), even transforming normally highly parental, monogamous males into inattentive fathers and polygamous mates (Raouf, Parker, Ketterson, Nolan, & Ziegenfus, 1997).

Relationships between circulating levels of T in adult male 2M and 2F Mongolian gerbils and their relative levels of sexual and parental effort (Clark, Tucker, & Galef, 1992; Clark, vom Saal, & Galef, 1992; Clark, Vonk, & Galef, 1998) are consistent with the hypothesis that in these rodents, as in the male birds that Ketterson and Nolan (1994, in press) described, there may be a T-mediated trade-off between sexual and parental effort. However, available evidence of effects of T on parental behavior of male gerbils is entirely correlational. In the present experiments, we experimentally manipulated levels of T in adult male Mongolian gerbils and examined effects of these manipulations on their parental behavior.

Experiment 1

We used several unobtrusive measures of male parental behavior to measure effects of circulating levels of T on the parental behavior of male gerbils. First, we determined the amount of time that males spent with pups when their mates were either present in or away from the nest. Although time in contact with pups is not necessarily a measure of parental behavior (e.g., males might be motivated to remain in the nest or in contact with their mates and only inadvertently contact young; Clark et al., 1998), it has been used previously either alone (e.g., Grota & 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 behavior in several rodent species. We also used two direct measures of parental behavior: the frequency with which males huddled over pups and the frequency with which males licked pups.

While observing parental behaviors that male and female gerbils directed toward young, we occasionally saw males mount and attempt to copulate with their partners. Following postpartum estrus, the vagina of female Mongolian gerbils seals and remains sealed throughout lactation. Consequently, most attempts by males to copulate with lactating females are unsuccessful, and mounting of lactating females by males is not "reproductive" in the strict sense of the word. However, measurements of frequency of attempted copulations by males with different circulating levels of T did allow us to corroborate Yahr et al.'s (1979) and Ulibarri and Yahr's (1996) more systematic investigations of effects of circulating levels of T on reproductive efforts of adult male Mongolian gerbils.

Method

Subjects

We used as subjects 74 virgin male and 74 virgin female Mongolian gerbils (*Meriones unguiculatus*) selected from 120 litters born in the vivarium of the McMaster University Department of Psychology to third-generation descendants of breeding stock acquired from Tumblebrook Farm (Brookfield, MA). After we weaned the subjects at 35 days of age, we placed them in same-sex groups of 3 or 4 in opaque polypropylene cages (35 cm long × 30 cm wide × 15 cm high) housed in a temperature- and humidity-controlled colony room illuminated on a 12-hr light–dark cycle (lights on at 5 a.m.). Throughout life, all subjects had ad libitum access to Purina Rodent Laboratory Chow 5001 (Ralston-Purina, Woodstock, Ontario, Canada) and water.

When each subject was 50 days old, we randomly assigned it to one of six conditions, with the constraint that no 2 subjects from the same litter were assigned to the same condition. After group assignment, the subjects were undisturbed except (a) to clean their cages once every 2 weeks, (b) to perform surgery on the male subjects when they were either 50 or 90 days old, (c) to pair the female subjects with males from our breeding colony, and (d) to pair each male subject with a pregnant female on the day that the male subjects reached 110 days of age. As a result of these manipulations, some males were paired with females 60 days and others 20 days after surgery, and some males were exposed to T for 60 days and others for 20 days before they were paired with females.

Apparatus

Silastic implants. We implanted each subject with a Silastic capsule (Dow-Corning Silastic tubing: 7.0 mm in length, 1.2 mm outside diameter, and 0.6 mm inside diameter; Dow-Corning, Midland, MI, Catalog No. Dow 602-285), capped at each end with Dow-Corning Silastic Type A adhesive. Silastic capsules implanted in some males contained a 5-mm column of crystalline T (Steroids, Wilton, NH) that we knew, from previous studies, restored plasma T to 2.51 ± 0.25 ng/mL (Clark, Bishop, vom Saal, & Galef, 1993), a level comparable to that seen in intact male Mongolian gerbils 3 to 4 months of age (Probst, 1987). Other Silastic capsules implanted in some males were empty; all were incubated in isotonic saline solution for at least 48 hr before they were implanted.

Caging. During the experiment, each male–female pair and the young the pair was rearing were housed in a shoe-box cage measuring 35 cm long × 30 cm wide × 15 cm high. The top of each cage was closed with 1.3-cm hardware cloth, and its floor was covered with a layer of wood-chip bedding. Each cage also contained 5 g of cotton batting for subjects to use as nesting material.

Late in the pregnancy of the female member of each pair, we placed a nest box, measuring 28.0 cm long × 12.7 wide × 12.7 cm high, at one end of her home cage. This nest box, constructed of transparent Plexiglas and divided into two identical compartments separated by a 12.7-cm square transparent Plexiglas partition, had two entrance holes, 5 cm in diameter, that allowed the subjects to have direct access from the 23.3 × 30.0-cm open area of each cage into the nest-box compartments (see Figure 1). A third 5-cm diameter opening cut at the top of the partition divided the nest box into separate compartments and allowed the adult, but not the juvenile, gerbils to pass directly from one compartment to the other. Hinged lids made of transparent Plexiglas allowed the experimenter access to each compartment of the nest box, and holes drilled through these lids provided ventilation in the nest box.

Procedure

Surgical treatment of male subjects. Surgery was performed on 37 males at 50 days of age and on 37 additional males at 90 days of age. We anesthetized all 74 males by intraperitoneal injection with sodium pentobarbitol (30 mg/kg) and then gonadectomized each male (gonadectomy lowers T levels in adult male Mongolian gerbils to 0.14 ± 0.03 ng/mL; Clark et al., 1993). Immediately after surgery, we implanted a single Silastic capsule at the base of the back of the neck of each subject. An empty Silastic capsule was

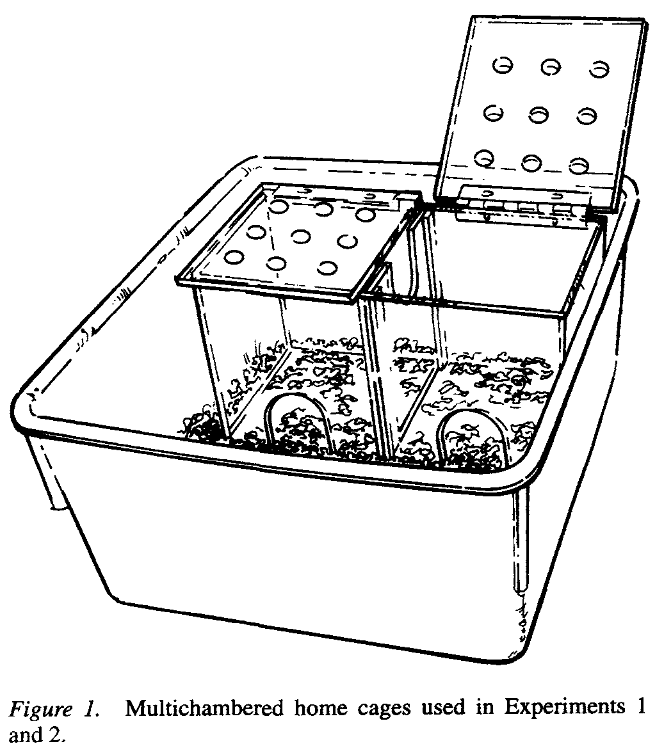

Figure 1. Multichambered home cages used in Experiments 1 and 2.

implanted in males assigned to two castrated groups that we gonadectomized either on Day 50 or on Day 90 (n = 13 per group), and a Silastic capsule containing crystalline T was implanted in males assigned to two T groups that we gonadectomized either on Day 50 or on Day 90 (n = 14 per group). Twenty subjects assigned to two intact groups that received sham operations either on Day 50 or on Day 90 (n = 10 per group) were anesthetized, shaved, incised, sutured, and implanted with an empty Silastic capsule.

Establishing pairs and composing litters. When each female subject reached 60 days of age, we placed her in the home cage of a reproductively proven adult male from our breeding colony and noted the date on which the pair first copulated, with the expectation that the female would deliver 25 days after they first had been observed to mate. Because, after surgical manipulation, we wished to treat males assigned to castrated, T, and intact groups identically, stud males were used to impregnate all females, even females that were to interact later with intact males.

Ten days before the expected day of delivery of each dam's litter, we removed the stud male from her cage. We then introduced one of the 74 male subjects into the cage of each pregnant female but separated from her by a hardware-cloth partition. The partition prevented aggression between the male and the female until they became familiar with one another. After the male and the female had been held apart for 24 hr, we removed the partition that separated them and placed a nest box (see Figure 1) in their cage.

Within 48 hr after removal of the partition, long before females delivered their young, interactions between pair mates were completely amicable, and newly formed pairs huddled and slept together in the same nest-box compartment. Their behavior was, at least to us, indistinguishable from that of a normal mated pair.

To control for effects of variation in the size or sex composition of the litters on the behavior of adult subjects (Clark & Galef, 1986; Elwood & Broom, 1978), on the day of a female's parturition, we removed her litter and replaced it with four male and four female foster pups taken from litters born on the same day that the female subject delivered her litter.

Observation of undisturbed adults and litters. On each day from Day 1 to Day 20 postpartum, 4 hr after light onset, an experimenter who was unaware of the group assignment of male pair members observed the 74 male subjects and their mates. The observer recorded once each 20 s, for 15 consecutive minutes, whether each adult was in physical contact with one or more members of its foster litter and, if not, whether the male and the female were in contact with one another. The experimenter also recorded at each inspection whether males were huddled over pups, whether they were licking pups, and whether they mounted their pair mates. 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 a male's attraction to the litter from male contacts with the litter that resulted from a male's attraction to his mate while she was in contact with the litter (Clark et al., 1997).

Verifying gonadectomy. On completion of Experiment 1, all males that had been gonadectomized were killed by injection with sodium pentobarbitol (50 mg/kg) and were examined to ensure that surgery had been successful.

Statistical Analyses

Differences among groups were first analyzed by using a 2 (age at treatment) × 3 (treatment) analysis of variance (ANOVA). Proportional data were arcsine transformed before analysis whenever variances were heterogeneous. Because we did not find either a main effect of age at surgical manipulation or an interaction between effects of age and effects of treatment on any dependent variable, to simplify presentation of data analyses in the text, we combined data across ages at surgery and performed one-way ANOVAs and subsequent post hoc least significant difference (LSD) tests.

Results

Data from four pairs assigned to the T group and two pairs assigned to the castrated group were not available because their litters died.

The upper portion of Table 1 presents the results of unobtrusive observations of the frequency with which male members of the gerbil pairs assigned to the T, castrated, and intact groups were seen in contact with their respective

Table 1
Experiment 1: Parental and Sexual Behaviors of Castrated, Intact, and Testosterone-Implanted (T) Males and Their Mates as a Function of Age at Surgery

Behavior	50 days old			90 days old		
	Castrated (n = 13)	T (n = 12)	Intact (n = 10)	Castrated (n = 11)	T (n = 12)	Intact (n = 10)
Males						
Pup contact[a]	$82.5_a \pm 1.9$	$58.9_b \pm 3.9$	$61.1_b \pm 3.2$	$79.4_a \pm 2.9$	$61.8_b \pm 3.7$	$62.6_b \pm 3.8$
Baby-sitting[a,b]	$77.9_a \pm 3.2$	$50.8_b \pm 3.9$	$60.8_b \pm 5.1$	$73.2_a \pm 5.0$	$57.5_b \pm 2.9$	$61.6_b \pm 3.3$
Mate contact[a]	$0.8_a \pm 0.1$	$3.7_b \pm 1.7$	$1.6_b \pm 0.3$	$1.0_a \pm 0.3$	$2.0_b \pm 0.4$	$2.6_b \pm 0.6$
Huddling over pups[a]	$27.3_a \pm 2.9$	$17.0_b \pm 3.4$	$18.0_b \pm 2.5$	$26.8_a \pm 2.6$	$14.8_b \pm 1.8$	$19.9_b \pm 1.9$
Licking pups[a]	$2.3_a \pm 0.3$	$1.3_b \pm 0.2$	$1.3_b \pm 0.4$	$2.2_a \pm 0.3$	$1.3_b \pm 0.3$	$1.3_b \pm 0.2$
Mean days males mounted females	$0.1_a \pm 0.1$	$1.3_b \pm 0.3$	$1.3_b \pm 0.6$	0	$0.8_b \pm 0.2$	$1.2_b \pm 0.5$
Females						
Pup contact[a]	74.8 ± 2.9	75.5 ± 3.5	75.2 ± 3.8	69.5 ± 3.3	72.6 ± 3.1	69.8 ± 3.4
Baby-sitting[a,b]	65.8 ± 3.6	69.8 ± 3.1	74.3 ± 4.0	64.5 ± 3.7	74.2 ± 3.3	71.9 ± 3.2

Note. Numbers are means ± standard errors of the means. Means within a row that refer to subjects of the same age that have different subscripts differ significantly at $p < .05$ in least significant difference tests.
[a]Percentage of 20-s intervals that subjects showed the behavior indicated. [b]Indicates when subjects were in contact with pups when their mates were not in contact with pups.

litters. Effects of treatment condition on contact time with pups were highly significant (one-way ANOVA), $F(1, 65) = 19.18$, $p < .001$, and castrated males that received empty Silastic implants were in contact with pups during a greater percentage of 20-s intervals than were either T males or intact males (LSD tests, both $ps < .01$). As Table 1 also shows, there was a significant effect of treatment on the percentage of 20-s intervals that males spent huddled over pups (one-way ANOVA), $F(2, 65) = 9.84$, $p < .001$, and castrated males were seen huddled over pups during a significantly greater percentage of 20-s intervals than were either T males or intact males (LSD tests, both $ps < .001$). Table 1 also shows significant effects of treatment on the percentage of 20-s intervals during which males were seen licking pups (one-way ANOVA), $F(2, 65) = 8.31, p < .001$, and castrated males were seen licking pups during a significantly greater percentage of 20-s intervals than were either T males or intact males (LSD tests, both $ps < .01$).

The frequency with which males remained in the nest with pups while their mates were not in contact with the pups (i.e., the percentage of 20-s intervals during which males "baby-sat" pups) also was affected by surgical treatment. Males assigned to castrated groups (those castrated and implanted with empty Silastic capsules) were significantly more likely to baby-sit than were males assigned to either of the other two treatments (one-way ANOVA), $F(2, 65) = 16.35, p < .001$ (LSD tests, both $ps < .01$). Clearly, the greater contact of castrated males than of intact or T males with pups was not the result of greater attraction of mates to castrated males than to intact or T males.

The low incidence of pup contact exhibited by T and intact males, relative to castrated males, was not due to differences in the behavior of their respective mates. As one can see in the lower portion of Table 1, which presents data describing the percentage of 20-s intervals during which females paired with castrated, T, and intact males contacted pups, there was no effect of male treatment on pup contact by their mates (two-way ANOVA), $F(2, 62) = 0.21$, *ns*.

Comparison of the data presented in the upper and lower portions of Table 1 reveals that castrated males both spent more time in contact with pups and baby-sat pups more frequently than did their mates, both $Fs(1, 44) > 10.57$, both $ps < .01$. In contrast, T males and intact males both contacted and baby-sat pups less frequently than did their female partners: for T males, both $Fs(1, 44) > 18.56$, both $ps < .001$; for intact males, both $Fs(1, 36) > 4.79$, both $ps < .05$.

Figure 2 shows the percentage of 20-s intervals during periods of unobtrusive observation that males assigned to the various conditions were seen in contact with pups. As is obvious from inspection of Figure 2, effects of treatment on probability of male contact with pups were particularly marked during the first 24 hr after pups' birth.

Differences in frequency of pup contact between intact and T males and castrated males were statistically reliable even when we excluded from the analysis data taken on Day 1 postpartum, when females were in estrus. On Days 2 to 20 postpartum, intact and T males were in contact with pups

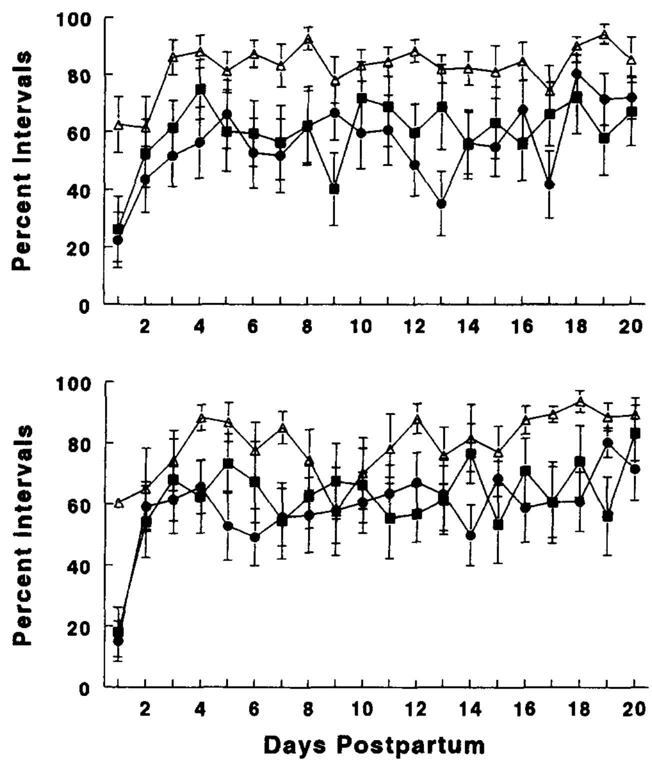

Figure 2. Mean percentage of 20-s intervals during 15-min periods of unobtrusive observation in Experiment 1 that castrated (open triangles), intact (filled circles), and testosterone-implanted (filled squares) males were in contact with a pup or pups. The upper panel shows the males that underwent surgery at 50 days of age; the lower panel shows the males that underwent surgery at 90 days of age. Vertical lines depict ± 1 *SEM*.

significantly less often than were castrated males (one-way ANOVA), $F(2, 65) = 15.48$, $p < .001$, and post hoc tests revealed that both intact and T males differed from castrated males in their frequencies of pup contact (LSD tests, both $ps < .01$).

Normal levels of plasma T did not inhibit paternal responsiveness by suppressing all social contact with conspecifics. To the contrary, as Table 1 shows, males with normal levels of T (intact males and T males) were in contact with their mates more frequently than were castrated males.

The frequency with which males interacted with females was affected by treatment condition. When data from males that underwent surgery at different ages were combined, there was a highly significant effect of treatment condition of males on frequency of contact with females (one-way ANOVA), $F(2, 65) = 7.83, p < .001$, and both T males and intact males interacted more, not less, frequently with their mates than did castrated males (LSD tests, both $ps < .05$).

As we expected on the basis of the reports of Yahr et al. (1979) and Ulibarri and Yahr (1996), male gerbils with normal levels of plasma T (T males and intact males) more frequently mounted their mates than did castrated males: 12 of 24 T males (50%), 9 of 20 intact males (45%), and only 1 of 26 castrated males (4%); they were seen mounting their female partners one or more times during the 20 days of observation, $\chi^2(1, N = 70)$ Yate's correction = 12.60, $p < .001$. This difference between groups remained significant even when we excluded data from the 1st day of observation, when females were in postpartum estrus, $\chi^2(1, N = 70)$ Yate's correction = 13.34, $p < .001$.

Discussion

The results of Experiment 1 show that gonadectomy, which produces a drastic reduction in circulating levels of T in male gerbils (Clark, vom Saal, & Galef, 1992), increased males' parental behavior and reduced their sexual behavior. Castrated males were more likely than males with normal circulating levels of T to be in contact with pups, to huddle over pups, to lick pups, and to remain with pups when their mates were away from the nest. In contrast, castrated males were less likely than males with normal circulating levels of T to mount their mates.

When assessing maternal effort, no one would hesitate to describe as more maternal females that (a) spend more time with pups, (b) are more likely to stay with pups when their mates are away from the nest, and (c) are more likely to huddle over and lick pups. It is consistent to describe castrated males showing a similar pattern of enhanced attention to pups as more paternal than either intact or T males.

Although T males and intact males appear to have avoided contact with pups immediately after the pups were born, castrated males were attentive to pups from the day the pups were born. Observations indicated that, on the day of birth, intact and T males would enter the nest, sniff the newborn pups, and immediately withdraw, whereas castrated males responded positively to pups, even on the 1st day young were present in the nest. The relatively low frequencies of pup contact exhibited by intact and T males were not due to dams excluding them from the nest site but rather to males' avoidance of the nest-box compartment containing the litter.

Unlike Elwood (1983), who suggested that "the male appears to be excluded from the nest by the female" (p. 251), we did not see females behave aggressively when their male partners entered the nest area, and no dam ever prevented a male from entering the nest. Furthermore, as part of a study of male participation in delivery of pups, we have been videotaping the behavior of pairs of gerbils throughout the 24 hr following the birth of a litter. Again, we have seen no aggression by females directed toward males and no exclusion by females of males from the nest compartment containing the litter.

The design of the present experiment required that we pair each female with a male other than the biological father of her litter, and we could not directly compare the parental behavior of foster and biological Mongolian gerbil fathers. It is therefore possible that the present results are unique to foster fathers. However, frequency of pup contact exhibited by foster fathers in the present experiment was very similar to that reported in the literature for biological fathers (Brown, Murdoch, Murphy, & Moger, 1995; Clark et al., 1998, Figure 2; Elwood, 1975; Ostermeyer & Elwood, 1984). There is, therefore, no reason to believe that foster and biological Mongolian gerbil fathers respond differently to conspecific young.

Castrated males in the present experiment, like those described in the literature (Ulibarri & Yahr, 1996; Yahr et al., 1979), also were less likely than males with normal circulating levels of T to attempt to mount their partners. Thus, males with normal circulating levels of T, whether in intact males or gonadectomized males whose levels of T had been artificially elevated (T males), showed both reduced parental effort and increased sexual effort. These findings are entirely consistent with the hypothesis that levels of plasma T mediate a trade-off between parental and sexual effort like that seen in adult male Mongolian gerbils from different IUPs (Clark et al., 1997).

Experiment 2

Carter and Roberts (1997) recommended testing animals for parental behavior in multichambered cages like those used in Experiment 1, because such cages allow subjects to retreat, should they choose to do so, from the stimuli emitted by young (see also Storey & Snow, 1987). Clark et al. (1998) suggested that because animals in multichambered cages are not forced into contact with their young and nest whenever they seek shelter, in multichambered cages attraction to young can be discriminated from attraction to shelter or nest site.

Results of a recent series of experiments carried out in a multichambered cage (Clark et al., 1998) showed that 2F male Mongolian gerbils spent more time with young than did 2M males, not because 2F males are more highly motivated than 2M males to remain in the nest, to remain under cover, or to remain near their mates, but because 2F males find young more attractive than do 2M males. In the present experiment, we asked whether this difference in the attractiveness of pups to male Mongolian gerbils from different IUPs, like differences in the tendency of males from different IUPs to remain in contact with pups, might be mediated by differences in circulating levels of T.

Method

Subjects and Apparatus

The subjects used in Experiment 2 were similar to those used in Experiment 1. The apparatus used in Experiment 2 was the same as that used in Experiment 1.

Procedure

Two hours after the end of the 15-min period of unobtrusive observation on the day that pups in a litter were 13 days old, each adult pair member was tested individually for its preference between pups and nest site. To perform such a test, we first removed both adults from their home cage and placed them in a holding cage. We then moved the eight pups that a pair was rearing from whichever nest-box compartment contained the nest and placed the entire litter on the opposite side of the partition that divided the nest box. We then waited 5 min before placing one adult in the open area of its home cage, facing away from the nest box. During the next 30 min, an observer, unaware of the group assignment of the male subjects, recorded the time that the parent spent in the nest-box compartment where the pups were now located and in the nest-box compartment containing the nest.

After the first parent had been tested, we removed it from the home cage, waited 5 min, and then introduced the other parent into the open area of the cage. During the next 30 min, an observer again recorded the time that the parent spent in each of the two compartments of the nest box. Order of testing of males and females in pairs was counterbalanced across litters. Each foster parent was awarded a preference score, calculated by dividing the number of minutes that it spent in the nest-box compartment with the pups by the total time that foster parent spent in both nest-box compartments.

Data Analyses

As in Experiment 1, we first analyzed the data by using a 2 × 3 ANOVA. Once again, because we did not find either a main effect of age or an interaction between age and treatment, we combined the data across ages at surgery and then performed one-way ANOVAs and post hoc LSD tests.

Results

One male subject retrieved his litter to the original nest site after the experimenter moved the pups to the other nest-box compartment, so we could not determine his preference between nest site and litter and therefore did not collect data from him.

As one can see in Table 2, which shows (a) the mean time during the 30-min test that male and female foster parents spent inside each of the two nest-box compartments, one containing the litter and the other containing the nest, and (b) the time that each foster parent spent in the nest-box compartment containing the pups as a percentage of the total time they spent in both nest-box compartments, treatment condition profoundly influenced males' behavior.

When data from males that were subject to surgical intervention at different ages were combined, there was a significant effect of treatment on the time males spent both in the compartment containing the nest (one-way ANOVA), $F(2, 64) = 4.81, p < .01$, and in the compartment containing the pups, $F(2, 64) = 6.14, p < .01$. Post hoc tests revealed that both T males and intact males spent significantly more time in the compartment containing the nest and significantly less time in the compartment containing the pups than did castrated males (LSD tests, both $ps < .05$). Consequently, treatment condition significantly affected the time that males spent in the nest-box compartment containing pups as a percentage of the total time males spent in both nest-box compartments, $F(2, 64) = 6.74, p < .003$. Both T males and intact males had a smaller preference for pups than did castrated males (LSD tests, both $ps < .001$). Furthermore, 14 of 24 castrated males spent more time with pups than in the nest site, whereas only 3 of 24 T males and 5 of 20 intact males did so, $\chi^2(2, N = 68) = 12.22, p < .003$.

As one also can see in Table 2, there was no effect of treatment of males on the behavior of females in the test situation. A significant proportion of females in all three groups preferred pups to nest site (binomial test, all $ps < .03$).

Discussion

The results of Experiment 2 are consistent with those of Experiment 1 and with the results of previous correlational studies of the relationship between IUP and the response of male gerbils to displacement of pups from the nest site (Clark et al., 1997). Males with low circulating levels of T, like females, were more attached to pups than to nest site; males with normal circulating levels of T were more attached to nest site than to pups. As Ketterson and Nolan (1994) proposed, high circulating levels of T appear to inhibit the response of males to young.

General Discussion

Ketterson and Nolan's (1994) Hypothesis

The results of both Experiments 1 and 2 indicate that normal circulating levels of T in adulthood depress parental responsiveness. The observations of sexual behavior reported in Experiment 1, together with information in the

Table 2
Experiment 2: Tests of Preference Between Pups and Nest Site

	50 days old			90 days old		
Behavior	Castrated (n = 13)	T (n = 12)	Intact (n = 10)	Castrated (n = 11)	T (n = 12)	Intact (n = 10)
Males						
Mean minutes with pups	$10.9_a \pm 2.2$	$5.2_b \pm 1.4$	$6.2_b \pm 2.3$	$12.5_a \pm 2.5$	$5.7_b \pm 0.9$	$6.1_b \pm 1.4$
Mean minutes in nest	8.2 ± 1.7	14.3 ± 1.8	13.5 ± 2.8	$8.1_a \pm 1.9$	$13.4_b \pm 1.7$	$12.5_b \pm 1.7$
% preferring pups	$54.2_a \pm 8.0$	$28.9_b \pm 6.8$	$34.0_b \pm 5.4$	$56.0_a \pm 10.2$	$30.1_b \pm 4.0$	$32.5_b \pm 6.1$
Females						
Mean minutes with pups	14.1 ± 2.2	16.9 ± 1.9	16.9 ± 1.5	15.4 ± 2.3	15.9 ± 0.9	13.7 ± 2.8
Mean minutes in nest	4.6 ± 0.9	5.8 ± 1.1	5.7 ± 2.1	6.2 ± 1.4	6.9 ± 0.9	5.5 ± 1.5
% preferring pups	72.8 ± 5.9	75.3 ± 5.9	77.0 ± 7.5	68.4 ± 6.4	70.3 ± 4.1	68.5 ± 9.8

Note. Numbers are means ± standard errors of the means. Means within a row that refer to subjects of the same age that have different subscripts differ significantly at $p < .05$ in least significant difference tests. T = testosterone-implanted.

literature (Ulibarri & Yahr, 1996; Yahr et al., 1979), indicate that increased circulating levels of T increase sexual activity in male Mongolian gerbils. Both results are consistent with Ketterson and Nolan's (1994, in press) hypothesized androgen-mediated trade-off between sexual and parental behaviors. Still stronger support for Ketterson and Nolan's hypothesis would be provided by evidence that graded increases in circulating levels of T in T-implanted, castrated male gerbils would result in graded decreases in their parental behavior and graded increases in their sexual behavior. Evidence that adult male gerbils from different IUPs that have different circulating levels of T exhibit trade-offs in their sexual and parental behaviors (Clark et al., 1997, 1998) suggests that castrated males provided with different amounts of exogenous T to create varying physiological levels of plasma T also would show graded trade-offs in their parental and sexual behaviors.

Intrauterine Position and Testosterone

The present results also provide a causal explanation for previous findings of a correlation between the IUPs of male gerbils and males' frequencies of sexual and parental behaviors (Clark et al., 1997). Differences in the parental and sexual behaviors of adult male gerbils (Clark et al., 1997) from different IUPs can be understood in terms of IUP effects on circulating levels of T in adulthood (Clark, vom Saal, & Galef, 1992).

Generality of Present Findings

Although the relationships among IUP, circulating levels of T, and parental and sexual effort appear to be fairly straightforward in male Mongolian gerbils, they may not be extrapolated uncritically to males of other rodent species. For example, as fetuses, male mice (*Mus domesticus*) from 2M IUPs have higher circulating levels of T than do their 2F brethren (vom Saal, 1989). However, in adulthood, male mice (unlike male gerbils) exhibit no correlation between IUP and circulating levels of T, and circulating levels of T in adult male mice do not appear to correlate with their paternal effort (Svare, Bartke, & Gandelman, 1977). Generally, effects of T on parental behaviors of male rats and mice reported in the literature are inconsistent and seem to depend to some extent on details of experimental procedure (Brown, 1985).

The most biologically relevant rodent species in which to examine effects of T on male parental behavior are those like the California mouse (*Peromyscus californicus*; Gubernick & Alberts, 1987) and the prairie vole (*Microtus ochrogaster*; Carter & Roberts, 1997), in which males normally engage in parental behavior. Unfortunately, little is known about the effects of T on paternal behavior in either species. Wang and De Vries (1993) reported that castration increases infanticide in male prairie voles, but measures of infanticide and of parental behavior need not be inversely related (Gubernick, 1994). We know of no experiments on effects of T on paternal behavior in California mice. Indeed, it would be interesting to examine whether Mongolian gerbils are unusual among rodent species whose males engage in parental behavior in the directness of effects of both IUP and T on males' care of conspecific young.

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Received December 7, 1998
Revision received March 31, 1999
Accepted April 5, 1999 ■

Acknowledgment of Ad Hoc Reviewers

The Editor thanks the following persons for reviewing manuscripts. (Numbers in parentheses indicate assistance with more than one manuscript.)

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