



Sexual motivation suppresses paternal behaviour of male gerbils during their mates' postpartum oestrus

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Adult male Mongolian gerbils, *Meriones unguiculatus*, avoid contact with their young on the day that the young are born. However, on succeeding days, fathers spend nearly as much time in contact with their offspring as do mothers. We undertook a series of studies to investigate the causes of the day-to-day change in male parental behaviour. In experiment 1, we tested males' response to pups before, after and on the day of their mates' parturition, and found that males were more parental both before and after the day of birth of their young than on that day. In experiment 2, we compared the parental behaviour of males paired either with intact or with ovariectomized dams (which do not come into postpartum oestrus) and found that males that were mated to intact females were less attentive to pups on the day of their birth than were the males mated to ovariectomized females. In experiment 3, we compared the parental responses of castrated and intact males to newborn pups and found that castrated males were more parental than intact males. In experiment 4, we compared the parental responses of males that were exposed to postpartum oestrous females but prevented from mating for 24 h. Extending the period of male sexual arousal to 24 h inhibited paternal responsiveness to neonates for 24 h. We interpret these results as being consistent with the hypothesis that on the day of birth of a litter, a male's parental behaviour is inhibited by the motivation to mate during his partner's postpartum oestrus.

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The parental activities of male and female Mongolian gerbils, *Meriones unguiculatus*, are very similar (Elwood 1983), except that male gerbils do not lactate and, like males of several other rodent species (e.g. grasshopper mouse, *Onychomys torridus*: McCarty & Southwick 1977; house mouse, *Mus musculus*: Pristnall & Young 1978), male gerbils do not participate in care of their young until the day following their birth (Elwood 1975; Clark & Galef 1999, 2000b).

This delayed onset of parental behaviour in male Mongolian gerbils does not result from females denying males access to the nest or young (Clark & Galef 2000b), as has been suggested for some other rodent species (red-backed voles, *Clethrionomys gapperi*: McGuire 1997; rats, *Rattus norvegicus*: Mennella & Moltz 1988; and, under some circumstances, meadow voles, *Microtus pennsylvanicus*: Storey et al. 1994). Review of videotapes of interactions of mated pairs in the hours following birth of their litter revealed no instances in which females chased or attacked their mates nor any indication that females inter-

fere with males approaching the nest and young (Clark & Galef 2000b; Clark et al. 2003).

In Mongolian gerbils (Norris & Adams 1981), as in many other biparental mammalian species, females are fertile following delivery of their young (prairie vole, *Microtus ochrogaster*: Richmond & Conway 1969; Witt et al. 1990; common marmoset, *Callithrix jacchus*: McNeilly et al. 1981; cottontop tamarin, *Saguinus oedipus*: Zeigler et al. 1987; California mouse, *Peromyscus californicus*: Gubernick 1988; Djungarian hamster, *Phodopus campbelli*: Reburn & Wynne-Edwards 1999). Consequently, on the day that the young are born, gerbil fathers must partition their reproductive effort between caring for current offspring and contributing to production of future descendants by copulating with their mates and guarding them from other males (Agren 1976, 1984, 1990; Roper & Polioudakis 1977; Agren et al. 1989).

In Mongolian gerbils, the need to inseminate females on the day they give birth is particularly pressing because a male failing to impregnate his partner during her postpartum oestrus will not be able to mate with her again until after she weans her young (Meckley & Ginther 1972; Clark et al. 1990). While female gerbils are nursing the young, their vaginas remain sealed, and intromission is impossible. Furthermore, mating in gerbils is unusually

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time consuming, lasting 3–8 h (Clark et al. 2003), and mating appears energetically costly as it involves six or seven ejaculatory series (Dewsbury 1981).

Given that male Mongolian gerbils should mate soon after their mates deliver and the demands on males of mating, it is perhaps not surprising that male gerbils ignore their newborn offspring and focus instead on inseminating and guarding their mates (Trivers 1972; Kleiman 1977; Dewsbury 1981). Indeed, one might expect development of behavioural mechanisms to inhibit parental behaviour of male gerbils during the postpartum period, when their mates are fertile and must be inseminated and guarded.

Here, we show (experiment 1) that male gerbils are ready to respond parentally to conspecific neonates during the last third of their mate's pregnancy, but that a male's parental response to young is suppressed after his mate gives birth. We show further (experiments 2, 3) that, during the postpartum period when male gerbils are not parental, both the presence of sexually arousing stimuli and a male's ability to experience sexual arousal are necessary for the suppression of his parental response to neonates. Last, we show (experiment 4) that artificially extending the duration of a pair's sexual motivation extends the period of inhibition of a male's parental response to newborn young.

EXPERIMENT 1: MALES' RESPONSES TO NEONATES ON DAYS SURROUNDING PARTURITION

In previous experiments, we found that male Mongolian gerbils fail to engage in parental behaviour until their young are 24 h old, after which male gerbils are nearly as attentive to their young as are their mates (Clark & Galef 2000b). We interpreted this finding in the most straightforward way, as indicating that in gerbils, onset of a male's parental behaviour is delayed until 24 h after his mate's parturition.

If onset of parental behaviour in male gerbils is, in fact, delayed until after delivery of young by their mates, then obviously, males should be indifferent to conspecific neonates before their mates give birth and begin to interact parentally with neonatal young only after their mates deliver young. In experiment 1, we investigated parental response in male Mongolian gerbils both before and after their mates gave birth to determine whether onset of responsiveness to conspecific young is delayed in male Mongolian gerbils.

Methods

Subjects

Subjects were 24 male and 24 female Mongolian gerbils, born and reared in the vivarium of the McMaster University Psychology Department. We weaned subjects at 32 days of age and placed them in same-sex groups of three or four in shoebox cages housed in a single temperature- and humidity-controlled colony room illu-

minated for 12 h/day (light onset at 0500 hours). Throughout the course of the experiment, all subjects had ad libitum access to pellets of Purina Rodent Laboratory Chow 5001 (Ralston-Purina, Woodstock, Ontario, Canada) and tap water.

When each male subject was 60 days old, we placed him with an unrelated virgin female, and left the breeding pairs undisturbed except to change cages every other week, and remove litters for weaning at 30 days of age. At the time of testing (see Procedure), breeding pairs were 6–8 months old and had raised two or three litters, but had not had any contact with pups for at least 30 days.

Apparatus

During the experiment, subjects lived in opaque, polypropylene shoebox cages, measuring $35 \times 30 \times 15$ cm. The top of each cage was closed with half-inch (1.3 cm) hardware cloth, and its floor was covered with a layer of wood-chip bedding. Ten days before the anticipated date of a female's parturition (see Procedure), we placed a nestbox, measuring $22.8 \times 12.7 \times 12.7$ cm, in each pair's cage (Fig. 1). Each nestbox, constructed of transparent Plexiglas and divided into two identical compartments by a 12.7×12.7 -cm transparent Plexiglas partition, had two entrance holes, 5 cm in diameter, that permitted subjects direct access to the nestbox compartments from the 23.3×30 -cm open area of the cage. A third 5-cm-diameter opening cut at the top of the partition divided the nestbox into separate compartments, permitting adults to pass directly from one nestbox compartment to the other. Hinged lids of transparent Plexiglas allowed experimenters access to each compartment, and holes drilled through these lids provided ventilation within the nestbox. When we placed a nestbox in a cage, we also provided its residents with 5 g of paper towelling for use as nesting material.

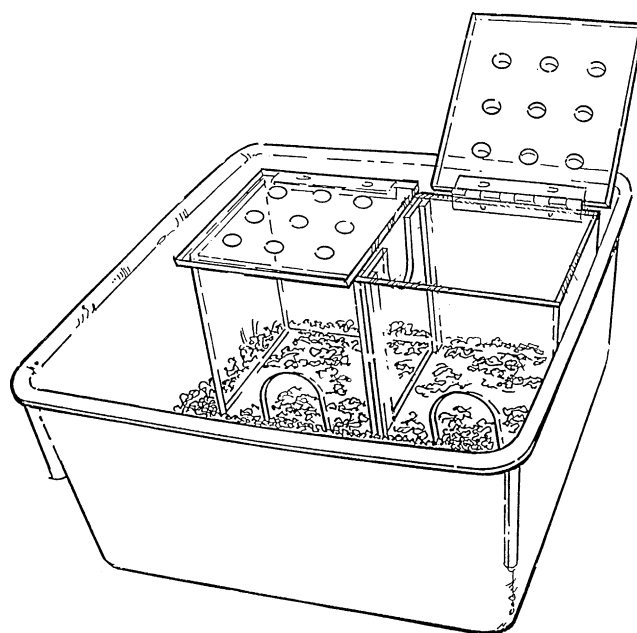


Figure 1. Home cage and nestbox used in all experiments (reprinted with permission from Elsevier: Clark et al. 2003).

Procedure

To determine the date of impregnation of female subjects, we observed each pair daily for 1–2 h before light offset, when gerbil females in oestrus mate. We recorded the date on which we observed copulation with the expectation that delivery would occur 25 days later.

Ten days before the predicted date of parturition, we inserted a nestbox into the cage containing an expectant female and her mate. Thereafter, we examined cages containing pregnant females twice daily (0800 and 1400 hours) for presence of a litter.

We randomly assigned males to one of two studies (studies 1, 2) that differed as to when we tested subjects' responses to unrelated newborn pups. In study 1, we tested each male's responses to pups 2–4 days before his mate's parturition, on the day his mate gave birth and on the day after his mate delivered. In study 2, to control for effects of repeated testing of males assigned to study 1, we tested each subject 5–8 days and 2–4 days before his mate delivered, and on the day his mate gave birth. We tested all subjects in both studies 3–6 h after light onset.

Assessing male responses to neonates. To test a male's response to newborn young, we first moved both adults and their litter (if present) to separate holding cages. We then placed three male and three female pups born in the preceding 24 h to a female in our breeding colony (sired by a male other than the subject male) in the nestbox compartment containing the subject's nest. After the pups had settled in the nest, we placed the adult male member of the pair in the open area of the home cage, facing away from the nestbox. For the next 30 min, an observer, who was unaware of the identity of the male being tested, recorded the time that the male spent in both nestbox compartments, one empty and the other containing the nest and six pups.

Assessing male sexual behaviour. To determine whether a pair mated during the female's postpartum oestrus, we observed each pair for 30 min at 1500 hours on the day that a female delivered her litter. Decades of experience of

breeding gerbils in our laboratory has revealed that such observation will determine whether a pair is engaged in the 3- to 8-h-long mating sequence that normally occurs during postpartum oestrus.

Data analysis

To simplify analysis of the data, we assigned each male subject a preference score based on the percentage of time that he spent in the nestbox compartment containing the nest and young relative to the total time he spent in both nestbox compartments. We analysed these preference scores separately for each study using repeated measures, one-way analyses of variance (ANOVAs).

Results

Males' preferences for the nestbox compartment containing pups were markedly affected by the reproductive state of their mates at the time of testing (repeated measures ANOVA: study 1: $F_{2,22} = 19.32$, $P < 0.001$; Fig. 2; study 2: $F_{2,22} = 9.31$, $P < 0.01$; Fig. 2), and males in both studies spent significantly less time with newborn young on the day their mates gave birth than before or after parturition (study 1: post hoc least significant difference, LSD, tests: both $P_s < 0.01$; study 2: post hoc LSD test: $P < 0.05$).

In study 1, prepartum preference scores of subjects did not differ from their postpartum preference score (LSD test: NS), prepartum and postpartum preference scores of individual males were correlated (Spearman rank correlation: $r_s = 0.65$, $N = 12$, $P < 0.05$), and we observed males mating on the day of parturition in 11 of 12 cages at 1500 hours. In study 2, preference scores of males tested 5–8 days before their mates' parturition did not differ from those of males tested 2–4 days before their mates gave birth (LSD test: NS), and we observed mating in 10 of 12 cages.

Discussion

The results of experiment 1 confirmed our previous finding that male gerbils tend to avoid contact with

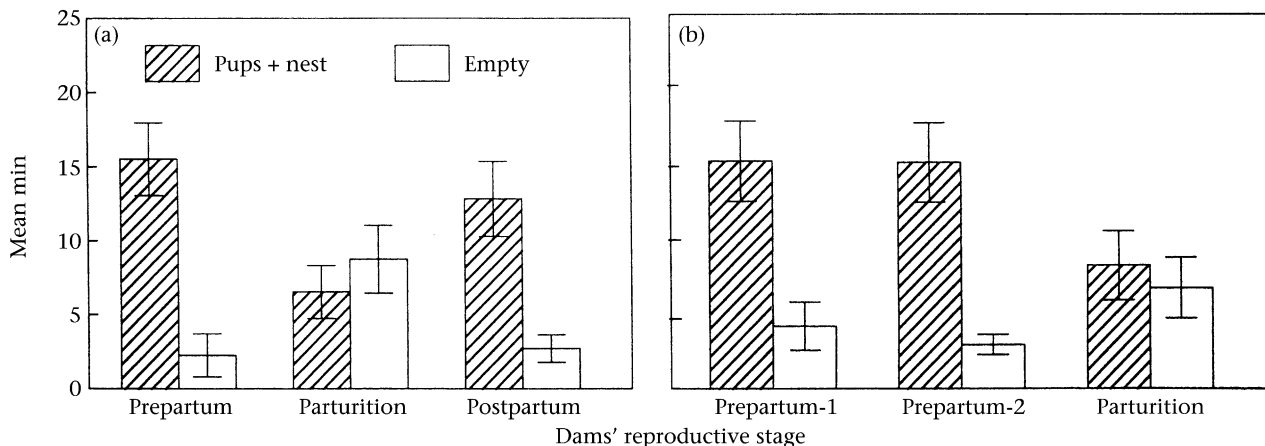


Figure 2. Mean \pm SE number of minutes out of 30 that male subjects spent in the empty nestbox compartment and the nestbox compartment containing the nest and newborn pups. (a) Study 1: males tested before their mates' parturition, on the day their mates gave birth and 24 h after their mates delivered. (b) Study 2: males tested both 5–8 and 2–4 days before their mates' parturition and on the day their mates gave birth.

neonates on the day of their birth (Clark & Galef 2000b; Clark et al. 2003). However, the finding in both studies 1 and 2 that male gerbils were responsive to neonatal pups before their own young were born is not consistent with our previous interpretation of this failure of male gerbils to respond parentally to their newborn young (Clark & Galef 2000b). If male gerbils are responsive to newborn young before their own offspring are delivered, failure of males to respond parentally to young on the day they are born cannot result from a delay in onset of male parental behaviour. Rather, the results of experiment 1 suggest that some event or events occurring around the time of parturition inhibit the expression of a parental response to young and that this inhibition develops in male gerbils well before their mates give birth.

Comparison of the results of studies 1 and 2 indicates that the lower preference scores of males in study 1 on the day of parturition did not result from repeated testing of males. Males in study 2, which received their second test of parental behaviour before their mates gave birth, did not show either an increase or a decline in preference score between tests 1 and 2.

Note, however, that while males were in the nestbox with pups after day 1, they maintained contact with the young, licked them and generally responded positively towards them. Thus, time in the nestbox compartment is a measure not only of attraction to pups but of responsiveness to them.

EXPERIMENT 2: EFFECTS OF POSTPARTUM OESTRUS ON MALES' PARENTAL BEHAVIOUR

The results of experiment 1 indicated that a male gerbil's parental behaviour is temporarily suppressed on the day his mate gives birth, and that recovery of a male's response to pups coincides roughly with termination of his mate's postpartum oestrus, 24–48 h after she delivers a litter (Norris & Adams 1981). Thus, the period during which males are unresponsive to pups is associated with both the appearance of pups and major changes in the hormonal status of their mates, reflecting termination of pregnancy and onset of postpartum oestrus.

In the present experiment, we determined whether males' response to pups on the day of their birth was inhibited by stimuli associated with the birth of a litter or oestrus in their mates. A female gerbil ovariectomized late in gestation, although capable of giving birth to the litter she is carrying at the time of surgery, cannot enter into postpartum oestrus. Consequently, examining responses to newborn pups of males mated to ovariectomized females on the day those females gave birth would allow us to differentiate effects on males' responsiveness to neonates of events accompanying parturition and onset of their mates' postpartum oestrus.

Methods

Subjects

Subjects were 20 breeding pairs of Mongolian gerbils, maintained in the vivarium of the McMaster Psychology Department as described in the *Methods* of experiment 1.

Procedure

Three to four days before the expected birth of a litter, we anaesthetized each female subject by intraperitoneal injection of sodium pentobarbital (50 mg/kg), shaved her flanks and made an incision through the skin and muscle of each flank. We bilaterally ovariectomized 10 females by extracting their ovaries through the incisions, then closed the incisions in all 20 females. As might be expected, ovariectomy had profound effects on pregnant females. It resulted in increased delivery of stillborn young, blocked normal maternal response to neonates, and most important for the present study, it blocked the occurrence of postpartum oestrus.

After surgery, we inspected each female's cage daily for presence of a litter, and on the day of her delivery, tested each female's male consort for his response to neonatal pups, as described in the *Methods* of experiment 1. The experimenter testing males was unaware of the treatment the males' partners had received.

After testing a male, we gave his mate's pups to an intact foster mother to rear (because ovariectomized female gerbils, like female rats, may fail to rear their young; Siegel & Rosenblatt 1975), and reunited females with their partners. To ensure that our surgery blocked oestrus in ovariectomized females, for 24 h following reunion of these females with their mates, we recorded their behaviour using a time-lapse video-cassette recorder (Panasonic AF 6720). We used dim red lights to facilitate video recording during the dark portion of the illumination cycle. We examined cages containing sham-operated females and their partners between 1400 and 1430 hours on the day of birth of their litter to determine whether mating was in progress.

Results and Discussion

During testing, mates of ovariectomized females spent more time in the compartment containing pups (Student's *t* test: $t_{18} = 2.60$, $P < 0.01$) and showed a greater preference for the nestbox compartment containing pups than did mates of sham-operated females ($t_{18} = 2.79$, $P < 0.01$; Fig. 3).

We observed all 10 males that were paired with sham-operated females copulating on the day of parturition, but saw no mating in videotapes of the 10 cages containing ovariectomized females and their mates.

Following birth of their litters, ovariectomized females did not enter postpartum oestrus, did not elicit sexual behaviour from mates and did not suppress their mates' responsiveness to neonatal young, whereas intact females entered postpartum oestrus, elicited sexual behaviour from mates and inhibited their mates' responsiveness to young. Whatever stimuli male gerbils are exposed to when a female gives birth do not, in themselves, affect males' responses to young. On the other hand, entry of a female into oestrus does suppress males' responses to young.

EXPERIMENT 3: EFFECTS OF CASTRATION

Taken together the results of experiments 1 and 2 suggest that exposure to an oestrous female suppresses male

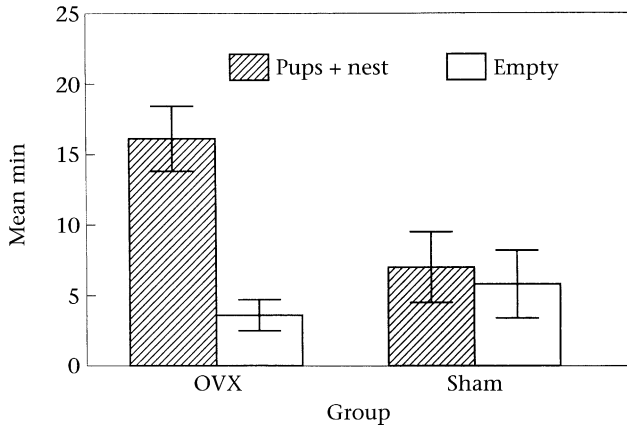


Figure 3. Mean \pm SE number of minutes out of 30 that males whose mates were either ovariectomized (OVX) or sham-operated before parturition spent in the empty nestbox compartment and the nestbox compartment containing the nest and neonates.

gerbils' parental response to neonatal pups. A reasonable interpretation of this inhibition of male gerbils' response to neonates is that male gerbils exposed simultaneously to an oestrous female and conspecific neonates experience conflicting motivations, and that the motivation to mate suppresses the motivation to attend to young. If so, eliminating a male's sexual motivation should allow him to respond positively to neonates even when interacting with a female in oestrus.

In the present experiment, we examined responses to newborn young of males cohabiting with females in post-partum oestrus when the males were either castrated or intact. If conflicting sexual and parental motivations cause temporary inhibition of males' responsiveness to neonates when their mates are in oestrus, then castrated males, which are not sexually motivated (Ulibarri & Yahr 1996), should not show reduced responsiveness to young on the day that young are delivered and females enter oestrus.

Methods

Subjects

Subjects were 30 male and 15 female Mongolian gerbils, born and reared in the vivarium of the McMaster University Psychology Department, as described in the Methods of experiment 1.

Apparatus

The apparatus was the same as that used in experiments 1 and 2.

Procedure

When subjects were 40 days of age, we formed 15 trios each consisting of two male and one female gerbil. Male gerbils 40 days of age are not yet sexually mature and cannot father litters.

Two days later, we injected both males in each trio subcutaneously with the analgesic buprenorphine (0.05 mg/kg) 15 min before inducing anaesthesia by intraperitoneal injection of sodium pentobarbital (60 mg/kg). We

then made incisions in the scrotum of each male and extracted the testes from one of each pair of males. We closed the incisions in both males and injected both subcutaneously with buprenorphine (0.05 mg/kg) 7 and 24 h after surgery.

On the day that the female member of each trio gave birth, we moved all three trio members and their litter from their home cage and placed them in separate holding cages. We then used the procedure described in the Methods of experiment 1 to test separately both the gonadectomized male and the biological father for their responses to unfamiliar newborn young. We counter-balanced the order of testing of males across trios, and the observer conducting tests was unaware of group assignment of the males that she tested.

Results and Discussion

We excluded two trios from the experiment: one because the sham-operated male in that trio was intolerant of its castrated member during the female's oestrus, and the second because, during testing, the sham-operated male attempted to harm a pup.

As in previous experiments, intact males spent little time with pups when tested on the day of their mates' parturition. As would be predicted on the basis of the hypothesis that sexual motivation underlies suppression of males' responsiveness to pups on the day their mates give birth, castrated males spent significantly more time in the compartment containing the pups (matched t test: $t_{11} = 4.03$, $P < 0.002$; Fig. 4), and significantly less time in the empty compartment ($t_{11} = 2.37$, $P < 0.04$; Fig. 4) than did their intact male trio-mates. Consequently, preference for pups was significantly greater in castrated males ($\bar{X} \pm \text{SE} = 82.7 \pm 3.9\%$) than in sham-operated males ($53.4 \pm 10.5\%$; matched t test: $t_{11} = 3.49$, $P < 0.006$). Clearly, the presence of a female in oestrus did not suppress castrated males' interest in offspring as it did for intact males.

It might be argued that the effect of castration on paternal behaviour that we observed was mediated by differences in the sexual experience of males assigned to castrated and intact groups. However, results of experiments with other rodent species (e.g. house mouse, *Mus domesticus*: Elwood 1986; prairie vole: Bamshad et al. 1994; reviewed in Brown 1993) and a series of experiments currently under way in our laboratory in which gerbils serve as subjects, indicate that sexual experience increases rather than decreases male rodents' parental responses to pups. Consequently, the increased paternal behaviour seen in castrated males in the present experiment cannot be attributed to castrated males having had less sexual experience than intact males before testing.

EXPERIMENT 4: MAINTAINING MALES' SEXUAL MOTIVATION

We found in experiment 1 (Fig. 2a) that, although male gerbils show little response to newborn young, 24 h after their mates deliver litters, males respond positively to

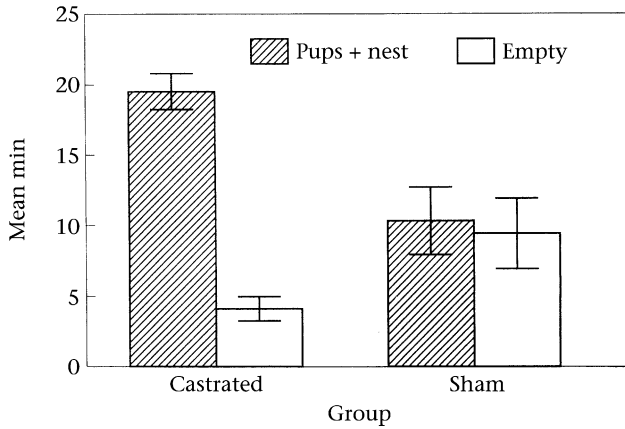


Figure 4. Mean \pm SE number of minutes out of 30 that castrated and sham-operated males spent in the empty nestbox compartment and the nestbox compartment containing the nest and newborn pups.

neonates, as they did in the days before their mates gave birth. If, as the results of experiments 2 and 3 suggest, restoration of males' parental response on the day after a litter is born results from decreased male sexual arousal following mating and termination of their partners' oestrus, then extending the period of a male's sexual arousal should extend the period of inhibition of his responsiveness to pups.

In intact pairs of gerbils, copulation begins after parturition, and continues for several hours, after which male gerbils, like males of other rodent species (Baum 1999), enter a refractory period during which they do not mate. To the best of our knowledge, the duration of the refractory period of male Mongolian gerbils has not been determined.

On the basis of the hypothesis that sexual motivation inhibits parental response of male gerbils, allowing males to copulate with their mates should increase their readiness to behave parentally towards young by both reducing males' sexual motivation and ending their mates' oestrus. Consequently, denying a male opportunity to mate whilst exposing him to a female in oestrus should extend the period during which he fails to respond parentally to conspecific young.

Methods

Subjects

Subjects were 45 breeding pairs of Mongolian gerbils, born and maintained in the vivarium of the McMaster Psychology Department, as described in the Methods of experiment 1. However, in the present experiment, to ensure that parenting did not interfere with mating, we removed litters from cages as soon as we found them and gave them to recently parturient females in our colony to rear.

Apparatus

The apparatus was the same as that used in experiments 1, 2 and 3.

Procedure

On the day of birth of a litter, after the litter had been removed, we randomly assigned each of the 45 breeding pairs to one of three conditions (remain, separate and remove; $N = 15/\text{condition}$) that differed in how males interacted with their mates. Each male assigned to the 'remain' condition stayed in his home cage with his recently parturient mate. Males assigned to the 'separate' condition remained in the home cage with their respective mates, but were separated from them by a half-inch (0.33 cm) screen partition that confined the female to the end of the cage opposite the nestbox and prevented pair members from mating. Each male assigned to the 'remove' condition remained in his home cage, but we removed his mate to a separate cage as soon as we discovered their litter.

Twenty-four hours after we found a litter in a pair's cage we tested each male for his preference between an empty nestbox chamber and one containing a nest and six unfamiliar newborn pups as described in the Methods of experiment 1. Just before testing a male assigned to the separate condition, we removed the female and screen partition from his cage.

At the conclusion of testing, we removed the litter of unfamiliar newborns and returned 10 of the 15 females assigned to the separate condition and five of the 15 females assigned to the remove condition to their mates. We then videotaped these 15 cages for 24 h, as described in the Methods of experiment 2.

Results and Discussion

Group assignment had a pronounced effect on males' responses to young (one-way ANOVA: $F_{2,42} = 6.77$, $P < 0.003$; Fig. 5), but had no effect on the time that males spent in the empty compartment (one-way ANOVA: $F_{2,42} = 1.65$, NS). Males assigned to the separate condition, which remained with their mates but were separated from them by a screen partition, spent less time in contact with pups than did males assigned to either the remain condition or the remove condition (LSD tests: both $P_s < 0.05$). Consequently, subjects assigned to the separate condition showed a marked reduction in preference for the nestbox chamber containing the pups ($\bar{X} \pm \text{SE} = 59.4 \pm 8.8\%$) relative to subjects assigned to either the remain condition ($80.0 \pm 7.7\%$) or the remove condition ($84.4 \pm 3.9\%$; one-way ANOVA: $F_{2,42} = 3.36$, $P < 0.03$; LSD tests: both $P_s < 0.05$). Removal of the female was as effective in reinstating a male's preference for pups as was mating with the female during her postpartum oestrus (LSD test: NS).

Nine of the 10 males assigned to the separate condition mated with their partners during the 24 h following reunion of the pair. Males started to mate from 2.1 min to 4.8 h after we reunited them with their mates ($\bar{X} \pm \text{SE} = 1.3 \pm 0.6$ h) and stopped mating 5.9 ± 0.50 h later. Mating was observed in only one of the five videotaped cages containing pairs assigned to the remove condition, and started 6 h after we reunited the pair.

Taken together, the results of the present experiment indicate that the presence of a sexually receptive female

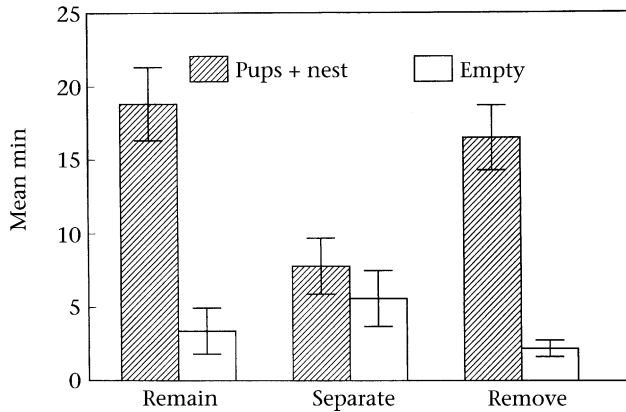


Figure 5. Mean \pm SE number of minutes out of 30 that males spent in the empty nestbox compartment and the nestbox compartment containing the nest and newborn pups during testing. Mates of males were either allowed to remain with the male and pups (remain), to remain with the male and pups but separated from them by a screen partition (separate) or removed from their mates' cages at parturition (remove).

inhibits the male's parental response to neonates, whereas mating (which we assume reduces males' sexual motivation) or removal of a sexually receptive female can terminate female-induced inhibition of male responsiveness to infants.

GENERAL DISCUSSION

The results of the present series of experiments show that, contrary to our previous working hypothesis, onset of parental behaviour is not delayed in male gerbils. Male gerbils are ready to care for young before their own young are born. However, their parental behaviour is temporarily suppressed on the day that their mates give birth. The present data also suggest that this temporary suppression of parental response is a result of heightened sexual motivation in male gerbils associated with the onset of postpartum oestrus in their mates.

We have previously provided evidence consistent with the view that, like some male birds (Wingfield et al. 1990; Ketterson & Nolan 1999), male Mongolian gerbils, show a lifelong, testosterone-mediated trade-off between sexual and parental effort. Male gerbils with chronically high circulating levels of testosterone are both more active sexually and less parental than are those with relatively low testosterone titres (Clark et al. 1997). The present results suggest that, in male Mongolian gerbils, this conflict between sexual and parental behaviour is expressed on brief as well as extended time scales. When mating opportunities arise, parental behaviours are suppressed.

Whether the pattern observed in male gerbils is typical of other biparental species is not known. In the literature, data describing males' interactions with their young during the perinatal period are often either not available or are collapsed across days (prairie vole: Oliveras & Novak 1986; Lonstein & De Vries 1999; California mouse:

Gubernick & Alberts 1987; Bester-Meredith et al. 1999; Djungarian hamster: Wynne-Edwards 1995), making it difficult to determine when males begin to behave parentally. However, in some biparental species, males have been reported to participate in delivery of their young, suggesting that they participate fully in care of the young on the day that their young are born (e.g. California mouse: Gubernick et al. 1994; Djungarian hamster: Jones & Wynne-Edwards 2000; spiny mouse, *Acomys cahirinus*: Makin & Porter 1984), although the role of testosterone in mediating paternal behaviour in some biparental rodent species (e.g. prairie vole: Lonstein & De Vries 1999; California mouse: Trainor & Marler 2002) may differ from that in Mongolian gerbils.

The exceptional duration of mating in Mongolian gerbils suggests a relatively high level of male–male competition in this colonial species (Kleiman 1977; Dewsbury 1981). In other rodents, such as prairie voles and deer mice, males finish mating with females in postpartum oestrus after achieving one to three ejaculations (Dewsbury 1974, 1981), suggesting lower levels of male–male competition. Consequently, conflict between mating and parental care may be less severe in other biparental rodents than it is in Mongolian gerbils, and temporary suppression of male parental behaviour during their mates' fertile periods may contribute less to reproductive success. An evolutionary history of extreme male–male competition may be the ultimate cause of temporary suppression of parental response in male gerbils.

Hormonal mediation of changes in the response of male rodents to neonates is relatively poorly explored. However, testosterone levels are known to rise in males in the presence of a receptive female (Bronson & Desjardins 1982), increase during mating (Kamel et al. 1977) and decline following mating (Batty 1978). Male gerbils show depressed levels of testosterone while they care for young (Brown et al. 1995), and chronically elevated levels of testosterone suppress paternal care (Clark & Galef 1999, 2000a). Thus, testosterone is a likely candidate for hormonal mediation of short-term trade-offs between parenting and mating in gerbils.

Regardless of the endocrine substrate underlying male Mongolian gerbils' parental behaviour and its temporary suppression by females in postpartum oestrus, the present results indicate that trade-offs between sexual and parental effort, previously found both in reproductive life histories of male gerbils (Clark et al. 1997) and during their development (Clark & Galef 2001), are also expressed in the day-to-day responsiveness of male gerbils to their mates and young. Under benign environmental conditions, such as those found in the typical laboratory, when motivations to mate and to care for young come into conflict, the former suppresses the latter.

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References

- Agren, G. 1976. Social and territorial behaviour in the Mongolian gerbil (*Meriones unguiculatus*) under seminatural conditions. *Biology of Behaviour*, **1**, 267–285.
- Agren, G. 1984. Pair formation in the Mongolian gerbil. *Animal Behaviour*, **32**, 528–535.
- Agren, G. 1990. Sperm competition, pregnancy initiation and litter size: influence of the amount of copulatory behaviour in Mongolian gerbils, *Meriones unguiculatus*. *Animal Behaviour*, **40**, 417–427.
- Agren, G., Zhou, Q. & Zhong, W. 1989. Ecology and social behaviour of Mongolian gerbils *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. *Animal Behaviour*, **37**, 11–27.
- Bamshad, M., Novak, M. A. & De Vries, G. J. 1994. Cohabitation alters vasopressin innervation and paternal behavior in prairie voles. *Physiology & Behavior*, **56**, 751–758.
- Batty, J. 1978. Acute changes in plasma testosterone levels and their relation to measures of sexual behaviour in the male mouse (*Mus musculus*). *Animal Behaviour*, **26**, 349–357.
- Baum, M. J. 1999. Mating behaviors, mammals. In: *Encyclopedia of Reproduction*, Vol. 3 (Ed. by E. Knobil & J. D. Neill), pp. 137–141. New York: Academic Press.
- Bester-Meredith, J. K., Young, L. J. & Marler, C. A. 1999. Species differences in paternal behavior and aggression in *Peromyscus* and their associations with vasopressin immunoreactivity and receptors. *Hormones and Behavior*, **36**, 25–38.
- Bronson, F. H. & Desjardins, C. 1982. Endocrine responses to sexual arousal in male mice. *Endocrinology*, **111**, 1286–1291.
- Brown, R. E. 1993. Hormonal and experiential factors influencing parental behaviour in male rodents: an integrative approach. *Behavioural Processes*, **30**, 1–28.
- Brown, R. E., Murdoch, T., Murphy, P. R. & Moger, W. H. 1995. Hormonal responses of male gerbils to stimuli from their mates and pups. *Hormones and Behavior*, **29**, 479–491.
- Clark, M. M. & Galef, B. G., Jr. 1999. A testosterone mediated trade-off between parental and sexual effort in male Mongolian gerbils. *Journal of Comparative Psychology*, **113**, 1–8.
- Clark, M. M. & Galef, B. G., Jr. 2000a. Why some male Mongolian gerbils may help at the nest: testosterone, asexuality and alloparenting. *Animal Behaviour*, **59**, 801–806.
- Clark, M. M. & Galef, B. G., Jr. 2000b. Effects of experience on the parental responses of male Mongolian gerbils. *Developmental Psychobiology*, **36**, 177–185.
- Clark, M. M. & Galef, B. G., Jr. 2001. Age related changes in parental responses of gerbils parallel changes in their testosterone concentrations. *Developmental Psychobiology*, **39**, 179–187.
- Clark, M. M., Bone, S. & Galef, B. G., Jr. 1990. Evidence of sex-biased postnatal maternal investment by Mongolian gerbils. *Animal Behaviour*, **39**, 735–744.
- 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., Whiskin, E. E. & Galef, B. G., Jr. 2003. Mongolian gerbil fathers avoid newborn male pups, but not female pups: olfactory control of early paternal behaviour. *Animal Behaviour*, **66**, 441–447.
- Dewsbury, D. A. 1974. Copulatory behaviour of California mice (*Peromyscus californicus*). *Brain, Behavior and Evolution*, **9**, 95–106.
- Dewsbury, D. A. 1981. An exercise in the prediction of monogamy in the field from laboratory data on 42 species of murid rodents. *Biologist*, **63**, 138–163.
- Elwood, R. W. 1975. Paternal and maternal behaviour in the Mongolian gerbil. *Animal Behaviour*, **23**, 766–772.
- Elwood, R. W. 1983. Parental care in rodents. In: *Parental Behaviour in Rodents* (Ed. by R. W. Elwood), pp. 235–257. New York: J. Wiley.
- Elwood, R. W. 1986. What makes male mice parental? *Behavioral and Neural Biology*, **46**, 54–63.
- Gubernick, D. J. 1988. Reproduction in the California mouse, *Peromyscus californicus*. *Journal of Mammalogy*, **69**, 857–860.
- Gubernick, D. J. & Alberts, J. R. 1987. The biparental care system of the California mouse, *Peromyscus californicus*. *Journal of Comparative Psychology*, **101**, 169–177.
- Gubernick, D. J., Schneider, K. A. & Jeannotte, L. A. 1994. Individual differences in the mechanisms underlying the onset and maintenance of paternal behavior and the inhibition of infanticide in the monogamous biparental California mouse, *Peromyscus californicus*. *Behavioral Ecology and Sociobiology*, **34**, 225–231.
- Jones, J. S. & Wynne-Edwards, K. E. 2000. Paternal hamsters mechanically assist the delivery, consume amniotic fluid and placenta, remove fetal membranes, and provide parental care during the birth process. *Hormones and Behavior*, **37**, 116–125.
- Kamel, F., Wright, W. W., Mock, E. J. & Frankel, A. I. 1977. The influences of mating and related stimuli on plasma levels of luteinizing hormone, follicle stimulating hormone, prolactin and testosterone in the rat. *Endocrinology*, **101**, 421–429.
- Ketterson, E. D. & Nolan, V., Jr. 1999. Adaptation, exaptation and constraint: a hormonal perspective. *American Naturalist*, **154**, S4–S25.
- Kleiman, D. G. 1977. Monogamy in mammals. *Quarterly Review of Biology*, **52**, 39–69.
- Lonstein, J. S. & De Vries, G. J. 1999. Comparison of the parental behaviour of pair-bonded female and male prairie voles (*Microtus ochrogaster*). *Physiology & Behavior*, **66**, 33–40.
- McCarty, R. & Southwick, C. H. 1977. Patterns of paternal care in two crested rodents, *Onychomys torridus* and *Peromyscus leucopus*. *Animal Behaviour*, **25**, 945–948.
- McGuire, B. 1997. Influence of father and pregnancy on maternal care in red-backed voles. *Journal of Mammalogy*, **78**, 839–849.
- McNeilly, A. S., Abbott, D. H., Lunn, S. F., Chambers, P. C. & Hearn, J. P. 1981. Plasma prolactin concentrations during the ovarian cycle and lactation and their relationship to return of fertility post partum in the common marmoset (*Callithrix jacchus*). *Journal of Reproduction and Fertility*, **62**, 353–360.
- Makin, J. W. & Porter, R. H. 1984. Paternal behavior in the spiny mouse (*Acomys cahirinus*). *Behavioral and Neural Biology*, **41**, 135–151.
- Meckley, P. E. & Ginther, O. J. 1972. Delayed nidation in lactating Mongolian gerbils. *American Journal of Veterinary Research*, **33**, 1247–1251.
- Mennella, J. A. & Moltz, H. 1988. Infanticide in rats: male strategy and female counterstrategy. *Physiology & Behavior*, **42**, 19–28.
- Norris, M. L. & Adams, C. E. 1981. Time of mating and associated changes in the vaginal smear of the post-parturient Mongolian gerbil (*Meriones unguiculatus*). *Laboratory Animals*, **15**, 193–198.
- Oliveras, D. & Novak, M. 1986. A comparison of paternal behaviour in the meadow vole *Microtus pennsylvanicus*, the pine vole *M. pinetorum* and the prairie vole *M. ochrogaster*. *Animal Behaviour*, **34**, 519–526.

- Pristnall, R. & Young, R.** 1978. An observational study of caretaking behavior of male and female mice housed together. *Developmental Psychobiology*, **11**, 23–30.
- Reburn, C. J. & Wynne-Edwards, K. E.** 1999. Hormonal changes in males of a naturally biparental and uniparental mammal. *Hormones and Behavior*, **35**, 163–176.
- Richmond, M. E. & Conway, C. H.** 1969. Management, breeding and reproductive performance of the vole, *Microtus ochrogaster* in a laboratory colony. *Laboratory Animal Care*, **19**, 80–87.
- Roper, T. J. & Polioudakis, E.** 1977. The behaviour of Mongolian gerbils in a seminatural environment, with special reference to ventral marking, dominance, and sociability. *Behaviour*, **61**, 207–237.
- Siegel, H. I. & Rosenblatt, J. S.** 1975. Estrogen-induced maternal behavior in hysterectomized–ovariectomized virgin rats. *Physiology & Behavior*, **14**, 465–471.
- Storey, A. E., Bradbury, C. G. & Joyce, T. L.** 1994. Nest attendance in male meadow voles: the role of the female in regulating male interaction with pups. *Animal Behaviour*, **49**, 1–10.
- Trainor, B. C. & Marler, C. A.** 2002. Testosterone promotes paternal behaviour in a monogamous mammal via conversion to oestrogen. *Proceedings of the Royal Society of London, Series B*, **269**, 823–829.
- Trivers, R. L.** 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. G. Campbell), pp. 136–179. Chicago: Aldine.
- Ulibarri, C. & Yahr, P.** 1996. Effects of androgens and estrogens on sexual differentiation of sexual behavior, scent marking and the sexually dimorphic area of the hypothalamus. *Hormones and Behavior*, **30**, 107–130.
- Wingfield, J. C., Hegner, R. E., Duffy, A. M. & Ball, G. F.** 1990. The ‘challenge hypothesis’ theoretical implications for patterns of testosterone secretion, mating systems and breeding strategies. *American Naturalist*, **136**, 829–846.
- Witt, D. M., Carter, C. S., Chayer, R. & Adams, K.** 1990. Patterns of behaviour during postpartum oestrus in prairie voles, *Microtus ochrogaster*. *Animal Behaviour*, **39**, 528–534.
- Wynne-Edwards, K.** 1995. Biparental care in Djungarian but not Siberian dwarf hamsters (*Phodopus*). *Animal Behaviour*, **50**, 1571–1585.
- Zeigler, T. E., Bridson, W. E., Snowdon, C. T. & Eman, S.** 1987. Urinary gonadotropin and estrogen excretion during the postpartum estrus, conception and pregnancy in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, **12**, 127–140.