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Parenting and potency: alternative routes to reproductive success in male Mongolian gerbils

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Abstract. Adult male Mongolian gerbils, *Meriones unguiculatus*, gestated in intrauterine positions between two female fetuses (2F males) are less likely than are adult males gestated between two male fetuses (2M males) to impregnate strange female gerbils with whom they are paired. The reduced copulatory success of 2F males is correlated with both lower circulating levels of and reduced sensitivity to testosterone. We asked whether 2F male gerbils compensated for their reduced copulatory success by increasing their parental effort. 2F male gerbils engaged in less sexual activity with their mates, but were more frequently in contact with pups than were 2M males, huddling over the young when their mates were absent from the nest. Although there were no differences in rates of survival or growth of pups reared by pairs consisting of a female and either a 2M or 2F male, mates of 2F males delivered significantly more pups as a consequence of copulations occurring during postpartum oestrus than did either mates of 2M males or females rearing young alone. We interpreted these results as consistent with Ketterson & Nolan's (1992, *Am. Nat. (Supplement)*, **140,** 533–562) hypothesis of a testosterone-mediated trade-off between investment in sexual and parental behaviours.

The copulatory success of male Mongolian gerbils, *Meriones unguiculatus*, is correlated with the intrauterine positions they occupied as fetuses; adult male gerbils gestated between male fetuses (2M males) are significantly more likely than are adult male gerbils gestated between female fetuses (2F males) to impregnate unfamiliar females with whom they are paired (Clark et al. 1992a).

The relatively low copulatory success of 2F male gerbils poses a conundrum. Why should natural selection have preserved genes that, when carried in fetuses gestated in 2F intrauterine positions (as are approximately 10% of gerbil fetuses), produce what appear to be reproductively disadvantaged phenotypes? Unless such genes produced some compensatory reproductive benefit, one would expect selection against them.

In a review of effects of testosterone on reproductive behaviours of birds, Ketterson & Nolan (1992, 1994) discussed a number of cases in which testosterone appears to increase sexual behaviour while decreasing parental effort (see also Wingfield et al. 1990). Ketterson & Nolan described such negative correlations between testosterone-sensitive traits as possible trade-offs that persist because they permit organisms to adjust their reproductive tactics in response to variations in local conditions.

There is reason to believe that the differing potencies of 2M and 2F male gerbils are mediated by differences in their circulating levels of testosterone. Adult male gerbils that occupied 2M intrauterine positions both have higher circulating levels of, and are more responsive to, testosterone than are adult males from 2F intrauterine positions (Clark et al. 1992b, 1993).

When exposed to conspecific young, male Mongolian gerbils, like male California deer mice, *Peromyscus californicus* (Gubernick & Alberts 1987), and male prairie voles, *Microtus ochrogaster* (Oliveras & Novak 1986), show all of the parental behaviours characteristic of their mates except, of course, for lactation (Elwood 1975, 1979), and there is evidence that the amount of parental behaviour shown by male gerbils may be

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affected by their circulating levels of testosterone (Brown et al. 1995).

In the present experiment, we explored the possibility that 2F male gerbils might compensate for their reduced potency by increasing the parental care they provide for those young that they do sire. Simultaneous observation of patterns of parental and sexual behaviour shown by male gerbils from known intrauterine positions, and measurement of the growth of young they helped to rear, provided an opportunity to assess effects of intrauterine position on male sexual and parental effort and the consequences of male parental effort for offspring growth and survival. Comparison of the reproductive success, resulting from copulations that occurred during postpartum oestrus, of females rearing young together with 2F or 2M males allowed assessment of effects of male intrauterine position on the parental investment of their female partners.

METHODS

Subjects

Subjects were 24 virgin male, 36 virgin female and 12 sexually proven, male Mongolian gerbils selected from 62 litters born in the vivarium of the McMaster University Department of Psychology (Hamilton, Ontario) to breeding stock acquired from Tumblebrook Farm (Brookfield, Massachusetts). Twelve of the 24 virgin male subjects had been gestated in 2M and 12 in 2F intrauterine positions. The remaining 12 male subjects and all 36 female subjects were delivered vaginally and reared by their natural dams.

Each virgin male subject was delivered by Caesarean section on day 24 of gestation, permanently marked for individual identification shortly after birth, then placed, along with its litter-mates, with a gerbil dam that had delivered vaginally on the day of birth of her foster litter (see also Clark & Galef 1988, 1992).

We weaned all subjects at 35 days of age. Until the start of the experiment (when males were 50 days old and females 45–50 days old), we housed 2M and 2F male subjects and all female subjects in groups of two to four siblings of the same sex in a temperature- and humidity-controlled colony room illuminated on a 12:12 h light:dark cycle (lights on at 0500 hours). After the remaining 12 male subjects reached 50 days of age, we used them as breeding stock for several months before they participated in the experiment.

General Procedure

We first placed each 2F and 2M male together with a virgin female in a shoe-box cage (35 × 30 × 15 cm) with a lid constructed of 1.3-cm hardware cloth and floor carpeted with a layer of wood-chip bedding. Each pair had ad libitum access to water and pellets of Purina Rodent Laboratory Chow 5001 (Ralston-Purina, Woodstock, Ontario) throughout the experiment.

When gerbils mate, they do so fairly continuously for several hours late in the afternoon, so we observed cages daily between 1400 and 1600 hours to see whether the male in each cage was mounting and attempting copulation with his female. We were thus able to determine the date of impregnation of all females.

To habituate each breeding pair to the presence of an observer before the start of the experiment, we began observing mated pairs 7 days before the expected date of parturition of each female, when the experiment actually started.

To control for effects of litter size and litter sex ratio on parental behaviour (Elwood & Broom 1978; Waring & Perper 1980; Clark & Galef 1992), on the day of parturition, we gave each pair a foster litter to rear comprised of four male and four female pups born within 24 h of delivery of a subject dam's own litter.

We undertook formal observations from the day of parturition (day 1) until day 20 post-partum, when pups became active in initiating contact with their parents (Kaplan & Hyland 1972).

During the experiment, we left parents and their foster litters undisturbed except for 15-min observation sessions conducted daily between 0800 and 1100 hours, cage cleaning, removal of pups for weighing on days 1 and 15 postpartum and removal of the male and litter from each dam's cage when her litter was 32 days of age.

Following removal of a male and litter, we examined each female's cage daily for birth of any litter conceived in postpartum oestrus, which in gerbils takes place during the 24 h immediately following delivery of a litter. Gerbils are capable of delaying implantation, so inter-litter intervals can considerably exceed the normal 25-day gestation (Norris & Adams 1971; Meckley & Ginther 1972).

We treated the 12 females that we paired with sexually proven males exactly as we treated the 24 females paired with 2M and 2F males, except that we removed the males from the cages of these 12 females 24 h after each female delivered her litter.

Observations

On each day from day 1 to day 20 postpartum, an observer, unaware of the intrauterine position that male subjects had occupied as fetuses, recorded behaviour. The observer looked at the animals in each cage once every 20 s and recorded on a prepared data sheet whether each adult in the cage was engaged in any of a variety of behaviours that we later categorized as either: (1) pup-directed, (2) mate-directed, (3) self-maintenance or (4) locomotor behaviour. Each category of behaviour is defined below.

Pup-directed behaviour was defined as behaviour during which an adult was in physical contact with one or more of the pups in its cage. Pup-directed behaviours included nursing pups, sprawling atop pups, huddling with pups, lateral contact with pups, carrying or rolling pups into the nest, licking or grooming pups and 'playing' with pups. We observed no aggressive behaviour directed by adults towards young, although two 2M males did mount their daughters before they were weaned.

Mate-directed behaviour was defined as behaviour involving physical contact between mates when they were not in contact with pups. Mate-directed behaviours included allogrooming, huddling with or over the mate and any attempts to mount and copulate with the mate. We observed no aggressive interactions between members of our mated pairs.

Self-maintenance behaviour included eating, drinking, self-grooming, sleeping and the gathering of nest materials by adults when not in physical contact with either pups or mate. Nest-building might, of course, be a pup-directed behaviour as well as one involved in self-maintenance (Dewsbury 1986), but it was sufficiently rare that its inclusion as a pup-directed behaviour, rather than as a self-maintenance behaviour, would not have affected our conclusions.

Locomotor behaviours were defined as those that involved movement about the cage, scratching at the walls of the cage, digging or scent-marking.

Measures of Contribution to Pup Development

We made both direct and indirect measurements of male contributions to pup development. Direct measures involved the determination of the number of foster young surviving to day 20 and the growth of pups from days 1–15 postpartum, when pups start to eat solid food. Indirect determinants of male contributions to pups involved measurement of the size of the litter each dam conceived during her postpartum oestrus (Clark et al. 1990a).

Data Analysis

We first assigned each animal a score for pup-directed, mate-directed, maintenance and locomotor behaviours equal to the number of 20-s intervals in which it had engaged in each category of behaviour. We then calculated the percentage of the 900 intervals (3/min × 15 min × 20 days) in which each subject had been classified as engaging in each of the four behavioural categories. Finally, we used an arcsine transformation to normalize the variances of these percentages.

There are problems with the most straightforward analysis of these data because the percentage scores for a subject in the four behavioural categories are not independent of one another; if a subject scored relatively high in one category, it must have scored relatively low in some other.

One approach to the problem posed by this lack of independence is to analyse only three of the four categories of behaviour for each group of subjects, although this approach does not fully solve the problem and is not strictly appropriate. A more rigorous although less easily communicated method is to transform the frequency counts into proportions using the following formulae: $Pr(B_1) = B_1/B_1 + B_2 + B_3 + B_4$, $Pr(B_2) = B_2/B_2 + B_3 + B_4$, $Pr(B_3) = B_3/B_3 + B_4$. Here $Pr(B_{1-N})$ equals the proportion of behaviours 1 to N, and B_{1-N} equals the observed number of occurrences of behaviours 1 to N (in the analysis we conducted for males, B_1 = mate-directed behaviours, B_2 = locomotor behaviour, B_3 = pup-directed behaviour and B_4 = self-maintenance behaviour; in the parallel analysis for females B_1 = maintenance behaviours, B_2 = locomotor behaviours, B_3 = pup-directed behaviours and B_4 = mate-directed behaviours).

Calculation of such proportions allows examination of differences between groups in each

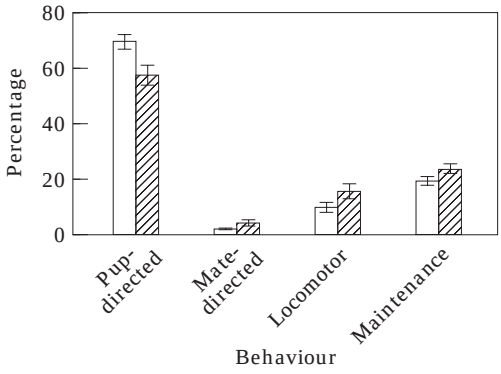

Figure 1. Mean ± percentage of 20-s intervals during which males gestated in 2F (□) and 2M (▨) intrauterine positions showed pup-directed, mate-directed, locomotor and self-maintenance behaviours.

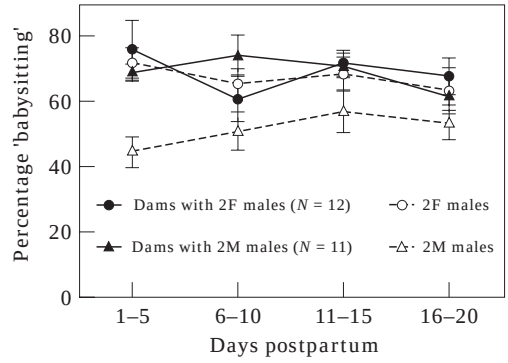

Figure 2. Mean ± SE percentage of 20-s intervals in which 2M and 2F males and their mates were in contact with pups while their mate was absent from the nest.

category of behaviour after controlling differences in the time allotted to preceding behaviours.

We performed both sets of calculations and reached the same statistical conclusions using each. Because the former method, although statistically less appropriate, is more easily communicated, we present and discuss below the results of Student's *t*-tests performed on arcsine transforms of the simple frequencies of occurrence of three categories of behaviour (pup-directed behaviour, mate-directed behaviour and locomotor behaviour) in both males and in females. Because of the lack of independence referred to above, data from the fourth category (maintenance behaviour) could not be meaningfully analysed statistically and are presented in Fig. 1 simply for completeness.

Data from one pair (a 2M male and his mate) were lost when its litter died.

RESULTS AND DISCUSSION

Do Males from 2M and 2F Intrauterine Positions Differ in Paternal Effort?

The behavioural profile of 2F males kept with a mate and litter differed significantly from that of 2M males maintained under the same conditions (Fig. 1). 2F males more frequently engaged in pup-directed behaviours than did 2M males ($t_{21}=2.19$, $P<0.04$), but 2M males had a higher frequency than did 2F males of both mate-directed ($t_{21}=2.50$, $P<0.02$) and locomotor behaviours ($t_{21}=2.03$, $P<0.05$).

The greater frequency of pup-directed behaviours seen in 2F males reflected primarily the greater frequency with which 2F males huddled over pups ($t_{21}=2.19$, $P<0.05$), and was not the result of more frequent casual, lateral contact with pups by 2F males while a male and pups were in a nest simultaneously ($t_{21}=0.15$, NS).

The most striking difference in pup-directed behaviours of 2M and 2F males was in the frequency with which 2F males remained in contact with pups while their mate was away from the litter and nest site (Fig. 2). Males from 2F intrauterine positions 'babysat' the young during an average of 67.8% of sampling periods when their mates were away from the litter; males from 2M intrauterine positions did so on an average of only 54.7% of available opportunities ($t_{21}=2.47$, $P<0.02$).

Observed differences in parental behaviour seen in 2M and 2F males were not due to differences in the behaviour of their respective mates (Fig. 3). Dams sharing a cage with 2F males showed pup-directed behaviours on no greater a percentage of occasions than did dams living with 2M males ($t_{21}=1.38$, $P>0.25$) and did not differ from dams living with 2M males in the percentage of occasions that they devoted to either locomotor ($t_{21}=0.81$, NS) or self-maintenance behaviours ($t_{21}=0.24$, NS). Consequently, it is difficult to attribute the observed difference in the 'babysitting' of 2M and 2F males (Fig. 2) to differences in the behaviour of their mates.

Male participation in rearing young did reduce the proportion of occasions on which dams engaged in one pup-directed behaviour. The 12

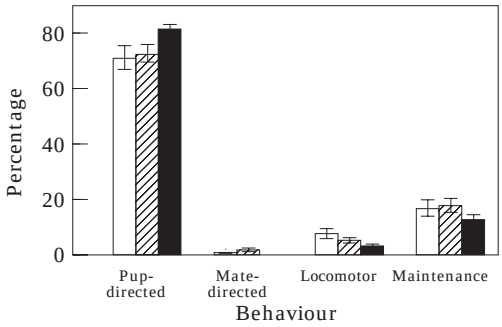

Figure 3. Mean ± SE percentage of 20-s intervals during which females mated to males gestated in 2F (□) and 2M (▨) intrauterine positions and dams without mates (■) showed pup-directed, mate-directed, locomotor and self-maintenance behaviours.

dams rearing young without males present in their cages nursed their young on a significantly greater proportion of occasions than did dams sharing their enclosures with either 2M or 2F males ($F_{2,32}=5.63$, $P<0.01$). However, there was no difference in the percentage of occasions on which females mated to 2M and 2F males nursed their young ($t_{21}=0.37$, NS).

Are 2M Male Gerbils More Sexually Active than 2F Male Gerbils?

Males from 2M intrauterine positions mated or attempted to mate on significantly more days than did males from 2F positions ($t_{21}=3.73$, $P<0.01$). Mounting was not restricted to the period of postpartum oestrus, but occurred throughout lactation, even though intromission was not possible except on the day of parturition and postpartum oestrus. The vagina of female gerbils seals closed shortly after birth and remains closed throughout lactation (Meckley & Ginther 1973; Clark & Galef 1992).

Do 2M Males Engage more Frequently in Behaviours Correlated with High Circulating Levels of Testosterone?

As we expected (Clark et al. 1990b), we observed 2M males scent-marking on significantly more days than 2F males ($t_{21}=2.74$, $P<0.01$) and, as noted above, 2M males engaged in significantly more locomotor behaviour than did 2F males. The higher frequencies both of scent-marking and of sexual activity seen in 2M than in 2F males each suggest that 2M males had higher circulating levels of testosterone than did 2F males (Thiessen et al. 1968; Baum 1993). These indirect indicators of plasma testosterone levels are consistent with the outcome of previous direct measurements of testosterone that show consistently greater levels of testosterone in 2M than in 2F adult male gerbils (Clark et al. 1992b).

Is there a Trade-off Between Parental and Mating Effort in 2F and 2M Male Gerbils?

As indicated in preceding sections, 2F males both attended more frequently to their foster young and engaged in less sexual activity than did 2M males. At a finer grain of analysis, the number of days on which individual males were sexually active was significantly negatively correlated with the number of 20-s intervals during which they engaged in pup-directed behaviours (Spearman's $r=-0.67$, $P<0.001$). Furthermore, the frequency with which a male scent-marked was (1) significantly positively correlated with the number of days on which he was observed engaged in sexual activity (Spearman's $r=0.48$, $P<0.02$) and (2) significantly negatively correlated with the number of 20-s intervals during which he showed pup-directed behaviours (Spearman's $r=-0.47$, $P<0.02$). These correlations suggest that high levels of testosterone are associated with high levels of sexual activity and low levels of parental behaviour, and are consistent with Ketterson & Nolan's (1992) hypothesis that testosterone levels mediate a trade-off between sexual and parental behaviours.

Do Differences in Parenting by 2M and 2F Males affect their Pups or Mates?

Direct measures

There were no differences in probability of survival or rate of growth of foster litters reared by dams alone and by dams paired with a 2M or 2F male (both $Fs_{2,32}<1.63$, NS).

Indirect measures

To control for differences in the reproductive capacity of individual females, we examined differences between the number of pups delivered by virgin females after they were paired with their respective mates for the first time (mating 1) and

Table I. Reproduction in response to copulations during postpartum oestrus by Mongolian gerbil dams that raised a litter either alone or with a 2F or a 2M male

	Dams with 2F males	Dams with 2M males	Dams alone
N	12	11	12
Size of first litter (litter 1)	6.4 ± 0.6	7.4 ± 0.5	6.9 ± 0.6
Size of litter resulting from all matings in postpartum oestrus (litter 2)	5.8 ± 0.9	3.2 ± 1.0	3.1 ± 1.0
% Females becoming pregnant in postpartum oestrus	75.0	54.5	50.0
Difference in number of pups delivered in litters 1 and 2	− 0.58 ± 0.8	− 4.1 ± 1.1	− 3.8 ± 1.1
Inter-birth interval (days)*	45.1 ± 1.9	44.5 ± 1.7	43.1 ± 1.3
Size at birth of litter conceived in postpartum oestrus (litter 2)*	7.8 ± 0.5	6.0 ± 0.7	5.3 ± 1.1

*Cell entries refer only to those females that gave birth to a litter conceived in postpartum oestrus.
Cell entries = mean ± SE.

the number of pups delivered as a consequence of copulations that occurred during postpartum oestrus (mating 2). Females that raised a foster litter either alone or together with a 2M male delivered significantly fewer pups following mating 2 than following mating 1 (Table I: paired *t*-tests: females alone $t_{11}=3.40$, $P<0.01$; females with a 2M male: $t_{10}=3.84$, $P<0.004$), but females mated with 2F males did not deliver significantly fewer pups following mating 2 than they had delivered following mating 1 (paired *t*-test: $t_{11}=0.73$, NS). Furthermore, there was a significant effect of male partner on the magnitude of the difference in number of pups delivered by females following matings 1 and 2 ($F_{2,32}=3.74$, $P<0.04$). Most important, a post hoc test revealed a significant difference between mates of 2M and 2F males (LSD test, $P<0.02$, as well as between mates of 2F males and females that reared their young alone (LSD test, $P<0.05$) in the size of the difference in number of pups females delivered as a result of matings 1 and 2 (Table I).

The reproductive capacity of mates of 2F males was reduced less by rearing the litter conceived in mating 1 than was the reproductive capacity of either the mates of 2M males or females that reared their young alone. We infer that females raising a litter with a 2F male invested less in that litter (Trivers 1972) than did females rearing a litter either alone or together with a 2M male.

GENERAL DISCUSSION

We undertook the present experiment to determine whether, as Ketterson & Nolan's (1992, 1994) reviews of the literature on avian reproduction suggested, there might be an androgen-mediated trade-off between reproductive competence and parental effort in male Mongolian gerbils. We found that males from 2F intrauterine positions, which are less likely to impregnate strange females with whom they are paired than are males from 2M positions (Clark et al. 1992a), interacted more frequently with pups than did males from 2M intrauterine positions and directed less sexual behaviour towards their mates than did males from 2M positions. Furthermore, the frequency of parental activity shown by an individual male was negatively correlated with his frequency of engaging in sexual behaviour. The results were, thus, consistent with the view that there is a trade-off between sexual and parental effort in male Mongolian gerbils.

Males from 2F intrauterine positions also scent-marked less frequently than did males from 2M intrauterine positions, a pattern of behaviour consistent with previous direct measurements indicating that 2F males have lower circulating levels of testosterone than do 2M males (Clark et al. 1992b). In the present experiment, we found significant correlations between males' frequencies of scent-marking, levels of parental behaviour and levels of sexual activity, suggesting that the trade-off between sexual and parental effort in male gerbils was androgen-mediated.

Last, the finding that presence of a 2F male, but not of a 2M male, increased the fecundity of females in response to copulations occurring during postpartum oestrus suggests that 2F males, but not 2M males, reduced the burden of pup

maintenance falling on the lactating females with whom they were paired.

Our failure to find any impact of the greater paternal effort made by 2M and 2F male gerbils on the survival or growth of young may reflect the lack of energetic challenges present in the laboratory and the consequent ability of females rearing young there to compensate for reduced parental effort of consorts. It remains to be determined whether direct effects of differences in the parental effort of 2M and 2F male gerbils on the well-being of pups in their care could be detected in less supportive circumstances than those under which we conducted the present experiment (Wynne-Edwards 1987; Wynne-Edwards & Lisk 1989; Gubernick et al. 1993).

The finding that mates of 2F males were more reproductively successful following copulation in postpartum oestrus than were mates of 2M males suggests that 2F males compensated for their reduced potency, relative to 2M males, in a manner we had not anticipated. 2F males appeared to have indirectly increased their own reproductive success by reducing costs to their mates of rearing young, thus directly increasing their mates' future fecundity and indirectly increasing their own.

The results of the present experiment suggest that 2F male gerbils may be more reproductively successful than 2M males as members of stable pairs, even though 2M males are demonstrably more reproductively capable than are 2F males when mating with a succession of unfamiliar females (Clark et al. 1992a). Relative reproductive success of male Mongolian gerbils from different intrauterine positions appears to be conditional upon whether a male mates promiscuously or enters into a long-term breeding relationship with a single female.

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