ANIMAL BEHAVIOUR, 2000, **59**, 801–806
doi:10.1006/anbe.1999.1365, available online at http://www.idealibrary.com on IDEAL®

Why some male Mongolian gerbils may help at the nest: testosterone, asexuality and alloparenting

MERTICE M. CLARK & BENNETT G. GALEF, JR
Department of Psychology, McMaster University

*(Received 14 June 1999; initial acceptance 15 August 1999;
final acceptance 11 November 1999; MS. number: A8517)*

In previous studies we have shown that those male Mongolian gerbils, *Meriones unguiculatus*, that as fetuses resided in intrauterine positions (IUPs) located between two female fetuses (2F males) have lower circulating levels of testosterone, less well-developed genital musculature, and lower reproductive success than males gestated in IUPs between two male fetuses (2M males). We have also found that such 2F males spend more time caring for conspecific young than do 2M males, and that presence of a 2F male, but not of a 2M male, with a lactating female and her litter decreases the cost to a dam of suckling one litter while gestating a second litter conceived in postpartum oestrus. Here we show that some 2F males, those with circulating levels of testosterone similar to those seen in females of their species, show no interest in females in oestrus and fail to impregnate females with which they are paired. Such 'asexual' 2F males spend 30–50% more time caring for nestlings than do sexually active 2F males. We suggest that such asexual, highly parental 2F males are incapable of direct reproduction and are obligate helpers at the nest that can contribute to their own fitness only by assisting to rear collateral kin.

More than 90% of female mammals rear their young without assistance (Kleiman & Malcolm 1981). However, in some mammalian species, males assist conspecific females to raise dependent juveniles (Alexander et al. 1991; Jennions & Macdonald 1994; Woodroffe & Vincent 1994; Carter & Roberts 1997; Moehlman & Hofer 1997). Sometimes such parental males are potential fathers of those they assist in rearing (Sussman & Garber 1987), but more often they are not (Woodroffe & Vincent 1994).

Nonpaternal male helpers are generally assumed to be temporarily unable to breed and to contribute indirectly to their own fitness by rearing collateral kin while awaiting a more promising environment in which to father offspring (Faulkes et al. 1989; Creel & Waser 1991). Here we provide evidence of testosterone-mediated variation in both the sexual and parental behaviour of male Mongolian gerbils, *Meriones unguiculatus*, that may have resulted in some male gerbils being permanent, rather than temporary, helpers at nests whose only contribution to fitness lies in rearing collateral kin.

Testosterone titres of adult male Mongolian gerbils vary by a factor of more than 10, from less than 0.35 to more than 3.72 ng/ml (Clark et al. 1992b; see also Probst 1985; Probst et al. 1987). Although this variance in testosterone titres has many potential causes, differing levels of intrauterine exposure of male fetuses to exogenous testosterone as a consequence of their intrauterine positions (IUPs) relative to members of the same and opposite sex is an important correlate of variance in testosterone titres of adult male Mongolian gerbils (vom Saal 1989; Clark et al. 1991, 1992b; Even et al. 1992). When adult, male gerbils that had gestated in IUPs between females (2F males) have, on average, circulating levels of testosterone half those of conspecific males gestated in IUPs between males (2M males; Clark et al. 1992b).

Fetal IUP predicts not only adult male gerbils' testosterone titres, but also the development of some of their reproductive anatomy. The bulbocavernosus muscle of adult male gerbils gestated in 2M IUPs are 50% heavier than those of their 2F brethren (Forger et al. 1996).

As might be expected, given that circulating levels of testosterone and weight of the bulbocavernosus muscle both correlate positively with sexual performance in male rodents (Sachs 1982; Hart & Melese-d'Hospital 1983), adult male gerbils from 2F IUPs show abnormalities in their mating behaviour (Clark et al. 1990), and are significantly less likely than are adult 2M males to impregnate unfamiliar females with which they are housed for several weeks (Clark et al. 1992a).

In male Mongolian gerbils, circulating levels of testosterone mediate variance not only in sexual behaviour, but in parental behaviour as well. Most male gerbils huddle over and groom young, generally engaging in the same

Correspondence: M. M. Clark, Department of Psychology, McMaster University, Hamilton, ON L8S 4K1, Canada (email: mclark@mcmaster.ca).

parental behaviours displayed by lactating females, except, of course, for lactation (Elwood 1975). However, 2F male gerbils (that have relatively low circulating levels of testosterone) are significantly more parental than are 2M male gerbils (Clark et al. 1998). Castration in either adulthood or adolescence significantly increases parental behaviour in male gerbils, and when testosterone titres of castrated males are returned to normal levels using Silastic implants of testosterone, parental behaviour decreases significantly (Clark & Galef 1999).

Differences in the parental behaviours of 2F and 2M male gerbils appear to affect the fecundity of females with which these males reside. At least under the relatively stress-free conditions of the laboratory, the parental activities of 2F males, but not those of 2M males, are correlated with subsequent increase in female reproductive success (Clark et al. 1997b).

Our previous results thus suggest that developmental history results in some male gerbils being unable to reproduce directly, some being exceptionally good alloparents, and some having exceptionally low circulating levels of testosterone. Here, we directly assess the correlation between testosterone level, parental behaviour, mating behaviour and reproductive competence in male gerbils.

In the first experiment, we determined the ability of 18 male Mongolian gerbils gestated in 2F IUPs to impregnate females with which they were paired. We then observed both the mating and parental behaviours of each of these 18 subjects. In a second experiment, we determined circulating levels of testosterone in a second group of 14 male gerbils from 2F IUPs whose fertility and mating behaviours we also measured. Thus, we could determine whether fertility, adequacy of mating behaviour and variation in frequency of parental behaviours were correlated with testosterone titres.

EXPERIMENT 1

We first determined the reproductive competence of each of 18 male gerbils from 2F IUPs, then examined both the mating behaviour and frequency of parental behaviour of each subject.

Methods

Subjects

Eighteen 2F male and 144 virgin female Mongolian gerbils that were third- or fourth-generation descendants of stock animals acquired from Tumblebrook Farm (Brookfield, Massachusetts) served as subjects. We had delivered the 18 male subjects, each taken from a different dam on the last day of pregnancy, by Caesarean section, and thus knew the IUP each had occupied during gestation.

Immediately following Caesarean delivery, we toe-clipped each male subject and his littermates for permanent identification, and then placed the entire litter with a foster mother that had delivered vaginally during the 24 h preceding delivery of the litter she was to rear (see Clark & Galef 1988 for details of Caesarean section and fostering).

We weaned subjects when they reached 32 days of age, after which we kept them in same-sex groups of three or four siblings until they were 60 days old, sexually mature and therefore, ready to participate in the experiment. The housing conditions we used after weaning not only assured that all subjects had equal sexual experience before the experiment started, but also allowed comparison with subjects that we had treated similarly in previous experiments.

Throughout the experiment, we maintained all subjects with ad libitum access to food (Purina Rodent Laboratory Chow 5001) and tap water in polypropylene shoebox cages, measuring 35 × 30 cm and 15 cm high, housed in a single colony room on a 12:12 h light:dark cycle, with controlled temperature and humidity.

Procedure

Measuring reproductive success. When each male subject was 60 days old, we paired him with a succession of three unrelated, sexually mature, vaginally delivered, virgin females from our colony. To start, we placed each male in a shoebox cage, measuring 35 × 30 cm and 15 cm high, with a virgin female, but separated from her by a screen partition. Twenty-four h later, we removed the partition and left the pair undisturbed (except for weekly examination and twice weekly cage cleaning) until a female was conspicuously pregnant or 30 days had elapsed. We have reported previously that 95% of 2M males impregnate females with which they are paired within 20 days (Clark et al. 1992a).

Measuring mating behaviour. One week after we had examined the male's reproductive competence, we observed his behaviour when placed briefly with the first of five females in artificially induced oestrus. We brought each female into oestrus by anaesthetizing her (Metofane; Janssen Pharmaceutica, North York, Ontario) and then implanting subcutaneously at the back of her neck a Silastic capsule (Dow-Corning Silastic tubing, 0.125 cm outside diameter, 0.06 cm inside diameter, capped at both ends with Dow-Corning Type A adhesive) that contained a 5 mm column of oestradiol benzoate (Ulibarri & Yahr 1996). In validating this procedure for inducing oestrus, Ulibarri & Yahr (1996) found, during 30 min observation periods, that each member of a random sample of 10 adult male gerbils paired with a treated female mounted and intromitted and that 9 of 10 ejaculated. We found similarly (unpublished observations) that each of 20 2M male gerbils placed with females in artificial oestrus induced using Ulibarri & Yahr's technique, mounted and 18 of the 20 both intromitted and ejaculated twice in 2 h.

Once each week, for 5 consecutive weeks, we placed each male subject in the home cage of a female in induced oestrus, but separated from her by a screen partition. Twenty-four h later, we removed the partition that separated the male and female. Then an observer, unaware of the previous reproductive success of subject

Table 1. Reproduction and parenting by 18 males in experiment 1 each tested with five females in induced oestrus, then observed for 20 days while with a litter and female

Mate	Yes	Yes	No
Impregnate	Yes	No	No
Number	8	6	4
Mean number of mounts	10.6 (2.6)	79.2 (42.5)	0
Mean number of intromissions	30.1 (3.3)	42.0 (10.4)	0
Latency to first ejaculate (min)	25.3 (3.4)	41.5 (8.3)	—
%Intervals brooding	40.4 (4.6)	40.2 (4.9)	58.6 (6.5)
%Intervals with pups/mate absent	67.2 (5.6)	66.2 (4.3)	87.8 (3.0)

Numbers in parentheses=1 SEM.

males, noted his behaviour towards the female until he either achieved two ejaculations or 2 h had passed. We used two ejaculations as a criterion for ending observation periods because Agren (1990) reported that two ejaculations from a single male is sufficient for impregnation.

Measuring parental behaviour. To measure the parental behaviour of each of the subjects whose reproductive success and mating behaviour we had observed, we placed each male individually in the cage of a female from our breeding colony when she was in the last week of her 25 day pregnancy. On each of the first 20 days postpartum, an observer who was unaware of the reproductive performance of the male, recorded, once every 20 s for 15 min, whether: (1) the male was crouched over the young in a nursing posture ('brooding the young'); and (2) the male was present in the nest and in contact with the young while the female was away from the nest and young (e.g. Clark et al. 1997, 1998). We have used the same procedures to sample parental behaviours of male and female gerbils in previous studies (e.g. Clark et al. 1997, 1998).

To equate the probability that females rearing young with potent and with asexual foster fathers from 2F IUPs would be both lactating and pregnant, on the day of parturition of each female we briefly returned her to the cage of the male that had sired her litter. Each female and her original mate remained together until the male achieved three ejaculations, which invariably occurred within 30 min. We then returned the female to the cage containing her litter and its foster father.

Results

Reproductive behaviour

Eight of the 18 male subjects succeeded in impregnating one or more of the virgin females with which they were paired; 10 failed to impregnate even one female.

Mating behaviour

The mating behaviour of four of the 10 males that had failed to impregnate females was severely compromised; none of these males mounted any of the five females in induced oestrus with which he was paired, and of course, none achieved intromission or ejaculation (Table 1). These four males also failed to show sexual interest in females in oestrus. Although the males sniffed the anogenital area of females, as they would have done to any unfamiliar conspecific, they did not pursue females about the cage and they did not attempt to mount them.

The remaining six males that failed to impregnate females mounted and intromitted frequently, and showed normal sexual interest in females, continually sniffing their anogenital areas and pursuing the females about the cage. During the five 2 h tests, one of these six males failed to ejaculate, four achieved one ejaculation on one or more of the five tests, and one achieved two ejaculations on two tests. Presumably, any male that mounted females and ejaculated had some chance of direct reproduction.

Parental behaviour

Males that failed to mount females in oestrus were significantly more likely than were males that mounted, both to assume a brooding posture over the pups (ANOVA: $F_{2,17}=4.57$, $P<0.03$; Table 1) and to remain with the pups when the dam was away from the nest ($F_{2,17}=5.15$, $P<0.02$; Table 1). Males that failed to mount females in oestrus and to impregnate females were significantly more parental than were either males that mounted females but failed to impregnate them or males that both mounted females and impregnated them (LSD test: both $P<0.05$).

Discussion

The results suggest a subset of 2F male Mongolian gerbils that fail to respond to oestrous females and are thus unable to reproduce; these males might be described as 'asexual' in that they show no interest in females in oestrus, fail to mount, intromit or ejaculate and are effectively sterile. Such asexual males spend almost 50% more time brooding young than do potentially fertile males and are almost one-third more likely than are sexually active males to stay in the nest with young when a lactating female leaves her young and nest site.

EXPERIMENT 2

To examine hormonal correlates of mating and parental behaviours in 2F male gerbils, we determined the testosterone titres of a second sample of 14 2F males whose reproductive performance and mating behaviour we had measured following the same methods used to measure

Table 2. Reproduction and testosterone titres of 14 males in experiment 2

Mate	Yes	Yes	No
Impregnate	Yes	No	No
Number	8	1	5
Mean number of mounts	27.5 (10.8)	166	0
Mean number of intromissions	68.7 (26.8)	61	0
Latency to first ejaculate (min)	33.5 (9.9)	68.2	—
T (ng/ml)	1.52 (0.13)	1.02	0.77 (0.12)

T: Testosterone. Numbers in parentheses=1 SEM.

parental behaviour of the 18 2F males participating in experiment 1.

Methods

Subjects

Our subjects were: 14 Caesarean-delivered male Mongolian gerbils from 2F IUPs, each born to a different dam; 42 unmanipulated, sexually mature, vaginally delivered virgin females; and 70 females brought into induced oestrus with subcutaneous Silastic implants of oestradiol benzoate.

Procedure

Between 1400 and 1600 hours, 2 weeks after we had finished evaluating each male's reproductive success and mating behaviour as in experiment 1, we anaesthetized each male by intraperitoneal injection with sodium pentobarbital (40 mg/kg) and collected a sample of blood by cardiac puncture. Testosterone levels of serum samples were then determined by radioimmunoassay (see Clark et al. 1993 for details of the bioassay).

Results

Reproductive and mating behaviour

Five of the 14 male subjects both failed to impregnate any of the three females with which they were paired and failed to mount any of the five females in induced oestrus with which they interacted; one male failed to impregnate any female but mounted and mated with four of five females in induced oestrus; and eight male subjects both sired litters and mated with females in induced oestrus.

Testosterone titres

Subject males that had failed to both mount females and sire litters had testosterone titres significantly lower than those males that had either sired litters, or mated with females in induced oestrus but failed to sire litters (Student's *t* test: t_{11}=3.88, P<0.03; Table 2). Indeed, the testosterone titres of the four asexual males examined were at the upper end of the range we have previously observed in female Mongolian gerbils (Clark et al. 1991).

GENERAL DISCUSSION

The results of experiments 1 and 2 indicate that, as a sequela of prenatal development in IUPs between two females, some male gerbils have circulating levels of testosterone in adulthood comparable to those seen in adult females of their species. Such 2F males are essentially asexual; they failed to either mate or reproduce, and such asexual males were significantly more responsive to conspecific young than were sexually active male gerbils that matured in 2F IUPs.

Integrating the present data with those reported in our previous studies (Clark et al. 1997, 1998; Clark & Galef 1999) shows that there is great variation in the frequency with which male gerbils engage in parental behaviour. For example, in a situation comparable to that used in the present experiment, 2M males spent an average ± SE of 57.8 ± 3.6% of observation periods in contact with young and 54.7 ± 2.6% of the time their partner was away from the nest with the pups, whereas 2F males did so on 70.2 ± 2.8 and 67.8 ± 3.7% of observation periods, respectively (Clark et al. 1998). As in the present experiments, even within 2F males there is considerable variability in parental responsiveness; asexual 2F males have unusually low testosterone titres and are significantly more parental than are sexually active 2F males.

An interesting question, though one on which our experiments cast no light, regards the selective pressures that might have resulted in the evolution of asexual male Mongolian gerbils. Given the current lack of evidence of the distribution of asexual, highly parental males among rodent species that occupy different ecological niches in nature, speculation as to the evolutionary causes of asexuality in male gerbils would be entirely post hoc and, therefore, not particularly compelling. It is, however, relevant to note that those who breed laboratory rats and mice find the occasional 'dud' male (Craig et al. 1959; Whalen et al. 1961) that fails to mate with any of a succession of females with which he is paired. We are not aware of any assessment of the parental behaviour of such sterile males, but their existence suggests that *M. unguiculatus* may not be the only rodent species with asexual males that can enhance their fitness only by helping to rear collateral kin.

For asexual males to enjoy reproductive success comparable to that of sexually active competitors, males' probability of direct reproduction would have to be relatively low and their probability of increasing their inclusive fitness by helping to rear kin would have to be relatively high. We know that: (1) gerbil dams can affect the level of prenatal exposure to testosterone received by their fetuses (Clark et al. 1991); (2) varying levels of prenatal exposure to testosterone effects testosterone titres in adulthood (Clark et al. 1992b); (3) adult circulating levels of testosterone effect the frequency with which males act parental. If having some asexual sons that care for their dam's or sisters' offspring contributes more to a dam's fitness than having only sons that reproduce directly, then selection might modulate the internal milieu of gerbil dams to produce some sons that develop as asexual, highly parental males.

In reviews of the literature on avian reproductive behaviour, Ketterson & Nolan (1994) discuss correlational evidence that testosterone increases sexual behaviour of birds while depressing their parental effort (Wingfield et al. 1990). For example, male pied kingfishers, *Ceryle rudis*, that help at the nest have significantly lower testosterone titres than do breeding males (Reyer et al. 1986). The present results suggest that in Mongolian gerbils, as in birds, circulating levels of testosterone may mediate a trade-off between sexual and parental behaviours (Clark & Galef 1999).

The correlations between intrauterine exposure to testosterone, testosterone titres in adulthood (Clark et al. 1992b), mating behaviour (Clark et al. 1992a) and expression of parental behaviours (Clark et al. 1998) revealed in the present and previous experiments suggest a relatively straightforward hormonal basis for both development and evolution of helping behaviour in male Mongolian gerbils.

Acknowledgments

We thank Fred vom Saal for performing radioimmunoassays and Jenifer Vonk, Dorothy DeSousa, Paul Ramos and Elaine Whiskin for technical assistance. This work was supported by the Natural Sciences and Engineering Research Council of Canada. The research presented here was described in Animal Utilization Proposal Nos 98-10-51, 97-11-55 and 96-11-88, approved on 1 December 1998, 6 January 1998 and 30 January 1997, respectively, by the McMaster University Research Ethics Board.

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