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Nursing one litter of Mongolian gerbils while pregnant with another: effects on daughters' mate attachment and fecundity

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Previous research has revealed profound effects of prenatal interactions among littermates on the subsequent fecundity and behaviour of female Mongolian gerbils, *Meriones unguiculatus*. Here, we determined whether interlitter competition for maternal resources similarly affects female phenotypes. We found that, when adult, female Mongolian gerbils whose dams were both nursing while gestating them and pregnant while suckling them (twice-challenged dams) were less likely to affiliate with their mates and less fecund than their peers reared by dams neither suckling a prior litter while gestating focal daughters nor pregnant with a subsequent litter while suckling them (not-challenged dams). Daughters of twice-challenged dams had smaller, more female-biased litters than did daughters of not-challenged dams, and the difference in behaviour of daughters of twice-challenged and not-challenged gerbil dams when choosing between their respective mates and unfamiliar males was as great as that seen in nominally monogamous and polygamous species of vole observed in similar circumstances. Our results suggest that the reproductive phenotype of females can be profoundly affected by naturally occurring variation in access to maternal resources that results from conflict between successive progeny in mammalian species where dams are sometimes both pregnant and nursing and sometimes neither pregnant with nor nursing one litter while rearing another.

In many litter-bearing mammals, hormonally mediated interactions between littermates while still in their dam's uterus affect both their reproductive biology and their parental behaviours as adults (vom Saal 1981; Clark & Galef 1998; vom Saal et al. 1999; Ryan & Vandenbergh 2002). Members of successive litters born to a mammalian dam can also interact with one another, albeit indirectly, because female mammals often suckle one litter while gestating its successor, thus setting the stage for competition between successive litters for the resources needed for growth and development that their dam provides (Mock & Parker 1997). Few studies, however, have examined possible effects of successive litters that are simultaneously gestated and suckled by a dam on each other's development, and those few have been limited to examination of effects of a gestated litter on the physical growth of

its nursing predecessor (e.g. Woodside et al. 1981; Martinez-Gomez et al. 2004). Here we found striking effects on the fecundity and social preferences of daughters in litters born to Mongolian gerbil, *Meriones unguiculatus*, dams that simultaneously suckled and gestated successive litters.

In their natural habitat, Mongolian gerbils rear several litters each year (Gromov 1992). In late winter, females give birth to their first litters of a reproductive season (Leont'ev 1954; Ochirov & Bashanov 1975). By definition, these first litters are gestated by dams that are not suckling a previous litter.

Many females are impregnated during the postpartum oestrus following delivery of their first litters, and thus, gestate their second litters of a season while suckling their first. Litters that are born at the height of the gerbil's breeding season, in the spring, should often be gestated by a dam that is suckling an older litter and then suckled by a dam gestating a younger litter.

In June, when the first burst of reproductive activity of free-living gerbils is ending (Leont'ev 1954), many females fail to reproduce and therefore suckle their early-summer litters while not pregnant with a successor litter. During

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the brief autumn breeding season, those females that do breed deliver only a single litter (Leont'ev 1954). Consequently, they are neither nursing while pregnant nor pregnant while nursing. Thus, like dams of many other mammalian species, Mongolian gerbil dams sometimes rear one litter at a time (if they fail to conceive during postpartum oestrus or lose a litter conceived during postpartum oestrus) and sometimes provide resources for two litters simultaneously, one gestating and one suckling.

Previous studies have revealed that the conditions experienced by Mongolian gerbils early in life profoundly affect their sexual, reproductive and parental behaviours as adults (reviewed in Clark & Galef 1995b; vom Saal et al. 1999). Although this earlier research focused on effects of intrauterine propinquity to male and female fetuses on adult phenotypes, it seems reasonable to suppose that other types of early experience might also affect the reproductive behaviours of gerbils. The present experiment was undertaken to determine whether some of the naturally occurring variation in the conditions in which litters of Mongolian gerbils are reared by their dams in the wild affects the reproductive phenotypes of daughters as adults.

In earlier work with Mongolian gerbils, we found effects of early experience on litter sizes, litter sex ratios, inter-litter intervals, maternal contact with young and mate attachment of females (Clark et al. 1986; Clark & Galef 1995a, 1998). We used the same measures in the present exploratory studies of the effects of challenges to gerbil mothers on their daughters' reproductive phenotypes. Limits on the resources available to us required separate studies of the effects of challenges to gerbil mothers on the reproductive profiles of their sons.

METHODS

Subjects

We used as dams 51 female Mongolian gerbils, each randomly selected from a litter born to one of 56 breeding pairs acquired from Charles River Canada (St Constant, Quebec) and reared in the vivarium of McMaster University's Department of Psychology. We manipulated the conditions under which these dams reared their third litters, and used as subjects a single female member of each of these 51 third litters ('daughters'). Offspring of dams other than the daughters used as subjects in this experiment served as subjects in other experiments not reported here.

Offspring of five of the original 56 dams were not used in the experiment. Two of these dams gave birth to third litters that contained no daughters, and three dams that we had randomly assigned to the twice-challenged condition (see Procedure) failed to become pregnant during the postpartum oestrus that followed birth of their third litters. To ensure that dams were not assigning themselves to conditions, we eliminated these three dams from the experiment rather than reassign them to the not-challenged condition (see Procedure).

Procedure

Selecting behavioural measures

We selected measures of adult reproductive and parental behaviour from among those known to be sensitive to effects of the intrauterine positions that female rodents occupied as fetuses (e.g. Clark et al. 1993; Vandenbergh & Huggett 1994; Clark & Galef 1995a).

Assignment of daughters to conditions

Although experimental manipulations involved the second and fourth litters delivered by each dam, we focused our investigation on the daughters in each dam's third litter. Daughters in dams' third litters were reared in one of four conditions in a 2×2 design (Table 1). Dams assigned to the twice-challenged condition ($N = 13$) both gestated their third litters while nursing their second litters and gestated their fourth litters while nursing their third litters. Consequently, twice-challenged dams had to provide resources for two litters both while pregnant with and while suckling third litters. Dams assigned to the not-challenged condition ($N = 10$) gestated their third litters while not suckling their second litters and suckled their third litters while not pregnant with their fourth litters. To create not-challenged dams, we removed their second litters at birth and removed their mates from their cages for 24 h following delivery of their third litters to prevent them conceiving their fourth litters.

We also examined daughters of dams challenged only once while rearing their third litters. Prenatally challenged daughters ($N = 14$) were reared by dams that suckled their second litters while gestating their third litters, but were not impregnated during the postpartum oestrus following birth of their third litters and therefore did not gestate fourth litters while suckling third litters. Postnatally challenged daughters ($N = 14$) were reared by dams that gestated their fourth litters while suckling their third litters, but had their second litters removed at birth (and given to other dams to rear) and therefore did not nurse their second litters while gestating their third litters.

Treatment of third litters

We weaned all third litters born to the 51 dams at 30 days of age, placed their female members in groups of two or three in opaque polypropylene cages ($35 \times 30 \times 15$ cm) and removed male littermates from the experiment. All animals had continuous access to tap water and pellets of Purina Rodent Laboratory Chow 5001 (Ralston-Purina, Woodstock, Ontario), and all resided in a single

Table 1. Conditions under which third litters (daughters) were reared

		Dams nursing second litter?	
		No	Yes
Dams gestating fourth litter?	No	Not-challenged	Prenatal challenge
	Yes	Postnatal challenge	Twice-challenged

temperature- and humidity-controlled colony room illuminated for 12 h each day.

When offspring reached 60 days of age, we randomly selected one female from the litter to serve as a subject in the experiment (a daughter), and placed her in a shoebox cage with a sexually proven male from our colony. When a daughter was conspicuously pregnant (in the third week of a 25-day gestation), we provided her and her mate with both nesting material and a nestbox ($28 \times 12.7 \times 12.7$ cm; Fig. 1). The nestbox consisted of two identical compartments separated by a transparent partition. Adults could enter each compartment from the open area of the cage or pass directly from one compartment to the other via an opening in the top of the partition separating the compartments that was placed too far above the cage floor for pups to reach.

Measuring mate attachment

Procedure. Before the mating associated with a daughter's postpartum oestrus following birth of her first litter began, we removed the male from the cage containing the daughter and her litter. Seven hours after a male was removed from the cage of a recently parturient daughter (when her postpartum oestrus had started), we determined the daughter's preference when given a choice between her mate and an unfamiliar male from our colony whose mate had given birth on the same day as had the subject female.

Apparatus. To measure a daughter's preference when choosing between her mate and an unfamiliar male, we examined her behaviour in a T-maze consisting of a start box with a sliding door connected to a 11.5-cm wide, 59-cm long alley that led to two 15.0-cm arms, each of which ended in an enclosure ($11.5 \times 11.5 \times 8$ cm). A partition of 0.5-inch (1.25-cm) hardware cloth separated each enclosure from the arm of the maze to which it was attached.

We first gave each daughter 10 min to explore the apparatus. At the end of this period of familiarization, we placed her in the start box, then placed her mate in one enclosure and an unfamiliar male from our colony in the other and opened the door confining the daughter in the start box. During the next 10 min, an observer, unaware of either the group assignment of daughters or the identity of males, recorded the time that each daughter spent within 7 cm of each of the two enclosures, one containing her mate and the other containing an unfamiliar male. After a daughter had been tested, we returned her and her partner to their home cage to mate.

Reproductive profile

When a daughter gave birth to her first and second litters (the second conceived during the postpartum oestrus associated with birth of her first litter), we determined the size, weight and sex of each pup, and the number of days between successive deliveries.
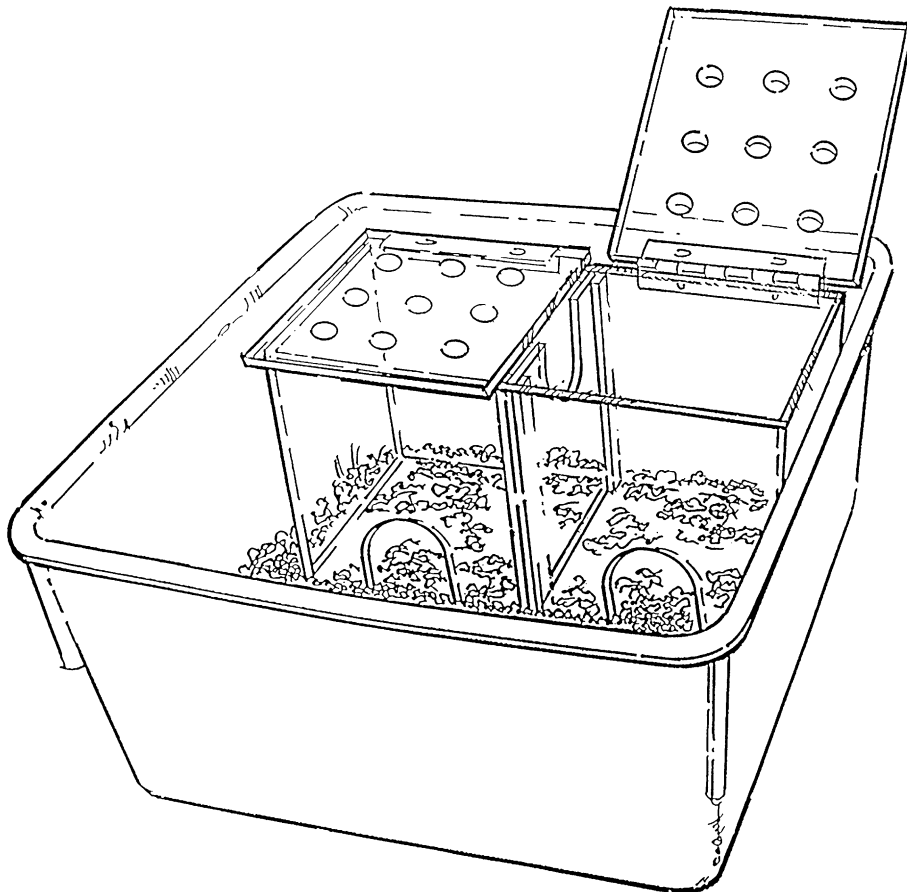

Figure 1. Home cage and nestbox used to measure parental behaviour of dams (reprinted with permission from Elsevier: Clark et al. 2002).

Maternal contact with young

Procedure. We examined the maternal behaviour of daughters following birth of their first litters. To control for effects of litter size and sex ratio on daughters' maternal behaviour (Elwood & Broom 1978; Clark et al. 1990) and subsequent reproduction (Norris & Adams 1981), on the day that each daughter delivered her first litter, we replaced her pups with a same-age foster litter of three male and three female pups born in our breeding colony. We observed the behaviour of daughters and their mates in their home cages, where we had placed a nestbox. Between 0800 and 1100 hours each day, from days 2 to 20 postpartum, an observer unaware of the group assignment of daughters recorded once every 20 s, for 15 consecutive minutes, both whether the daughter was in the nestbox compartment containing the nest and her foster litter and whether her mate was present.

Data Analysis

To redress the problem of range restriction, data on sex ratios of litters were arcsine-transformed before analysis, and data on number of intervals during which mothers were in contact with their young were converted to percentages and then arcsine-transformed.

RESULTS

Analyses

We randomly assigned mothers to each of the four conditions in a 2 (dams nursing) × 2 (dams gestating) design (Table 1). The usual way to present analyses of data from subjects in such a design is to begin with the outcome of the resulting 2 × 2 ANOVA. To facilitate presentation, we describe the results in two separate analyses. In the first, we compared the reproductive phenotypes of adult daughters from focal litters born to and suckled by twice-challenged and not-challenged dams to evaluate effects of challenges experienced by dams on daughters in third litters. In the second, we compared the reproductive phenotypes of daughters in focal litters born to dams randomly assigned to all four conditions to get an indication of the stage in development when maternal effects on the adult reproductive phenotypes of daughters in third litters were most pronounced. The sole unusual feature of the presentation of the data is that we begin with comparison of two of the groups within a 2 × 2 design and then consider the overall analysis, rather than the reverse.

Reproductive Profiles

We found no differences in first litters produced by daughters born to twice-challenged and not-challenged dams (Table 2). However, when daughters born to twice-challenged dams were themselves challenged by the need to gestate their second litters while nursing their first, profound effects of the rearing conditions of daughters on both interlitter intervals and the size and sex composition of second litters were revealed (Table 2).

Table 2. Effects of dams' challenges on their daughters' reproduction

Daughters	Dams			
	Twice-challenged	Not-challenged	Prenatal challenge	Postnatal challenge
Litter 1				
N	13	10	14	14
Litter size	6.0±0.6	6.0±0.5	6.3±0.5	5.7±0.6
Weight (g)	2.9±0.2	3.1±0.1	3.0±0.1	2.9±0.2
Sex ratio	51.0±7.0	42.6±5.1	46.6±6.3	54.2±5.7
Litter 2				
N	13	10	14	12
Interval (days)	42.5±0.8	38.4±1.1	42.7±1.2	37.9±1.1
Litter size	6.0±0.4	7.3±0.4	6.6±0.4	5.7±0.6
Weight (g)	3.2±0.8	3.2±0.1	3.3±0.1	3.1±0.6
Sex ratio	36.0±4.6	50.0±4.0	48.0±4.4	50.9±4.0

Table entries are means ± SE.

Second litters of daughters of twice-challenged dams had significantly longer interlitter intervals and both smaller second litters and more female-biased second litters than did daughters of not-challenged dams (Student's t test: all $ts_{20} > 2.20$, all $Ps < 0.04$). Both the size and sex ratios (percentage of males in a litter/100) of daughters' second litters were affected by postnatal challenge (twice-challenged and postnatal challenged groups) to their dams (ANOVA: $Fs_{1,43} > 5.90$, both NS), but neither prenatal challenge (twice-challenged and prenatal challenged groups; both $Fs_{1,43} < 1.15$, both NS) nor the interaction between prenatal and postnatal challenge (both $Fs_{1,43} < 0.50$, NS) significantly influenced the size or sex ratios of daughters' second litters.

Parental Contact

On days 2–20 following birth of their first litters, daughters of twice-challenged dams spent significantly less time in the nest with their pups and mate than did daughters of not-challenged dams (Student's t test: $t_{21} = 2.59$, $P < 0.01$; Fig. 2). Again, daughters' behaviour was significantly affected by postnatal challenge to their dams (ANOVA: $Fs_{1,47} = 5.51$, $P < 0.05$), but was not affected by either prenatal challenge ($F_{1,47} = 1.75$, $P = 0.19$) or the interaction between prenatal and postnatal challenge ($F_{1,47} = 3.44$, $P = 0.07$). On the other hand, daughters of twice-challenged dams were in the nest alone with their pups significantly more often than were daughters of not-challenged dams ($t_{21} = 2.36$, $P < 0.03$; Fig. 2). Consequently, the total time that daughters of twice-challenged and not-challenged dams spent with their first litters did not differ ($t_{21} = 1.02$, $P = 0.32$; Fig. 2).

The differences between the number of times twice-challenged and not-challenged dams were seen alone with their pups and in the nest together with their mate and pups reflected differences in the number of times that mates of not-challenged ($\overline{X} \pm$ SE = 39.2± 0.8 observations/day) and twice-challenged (31.0 ± 1.1 observations/day) dams were seen in the nest with the
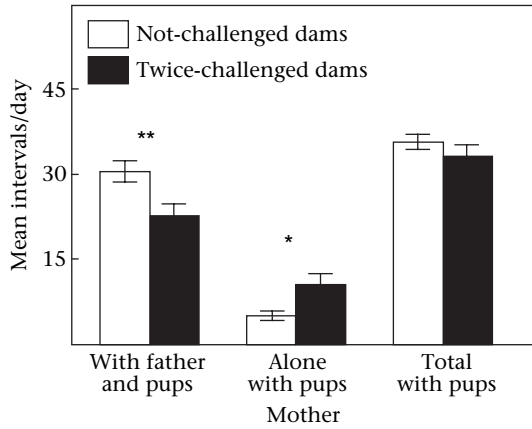
Figure 2. Mean ± SE intervals/day on days 2–20 postpartum that daughters of not-challenged and twice-challenged dams were seen in the nestbox alone with the pups, together with their mate and pups, and in total with pups: *$P < 0.05$; **$P < 0.01$.

Figure 3. Mean time ± SE that daughters spent within 7 cm of their mates as a percentage of time that they spent within 7 cm of both their mate and a strange male. Dashed line represents indifference: *$P < 0.05$.

pups ($t_{21} = 2.50, P < 0.02$). However, our observations were not sufficient to determine whether twice-challenged females were excluding their mates from contact with the pups, or whether the mates of twice-challenged females were less likely than were the mates of not-challenged females to enter or remain in the nest when their mates were there.

Mate Attachment

Preferences of two females for their respective mates could not be assessed because no pairs in our colony gave birth on the day that litters were born to focal pairs.

When offered a choice between their respective mates and a randomly selected unfamiliar male, daughters of twice-challenged dams were significantly more likely than were daughters of not-challenged dams to prefer the unfamiliar male (Student's t test: $t_{21} = 2.32, P < 0.03$; Fig. 3). There was a significant effect of postnatal challenge to dams (ANOVA: $F_{1,45} = 5.9, P < 0.03$), but no significant effect of prenatal challenge ($F_{1,45} = 0.96, P = 0.33$), and no significant interaction between prenatal and postnatal challenge ($F_{1,45} = 0.60, P = 0.44$).

DISCUSSION

Taken together the present results indicate that indirect interactions between successive litters, like direct interactions between members of a single litter, can have biologically important effects on the development and consequent reproductive profile of female Mongolian gerbils. Daughters in third litters whose dams were required both to nurse their second litters while gestating their third and to gestate their fourth litters while suckling their third were less fecund and less likely to prefer to associate with their mates than were daughters of third litters whose dams raised them without competition from other litters.
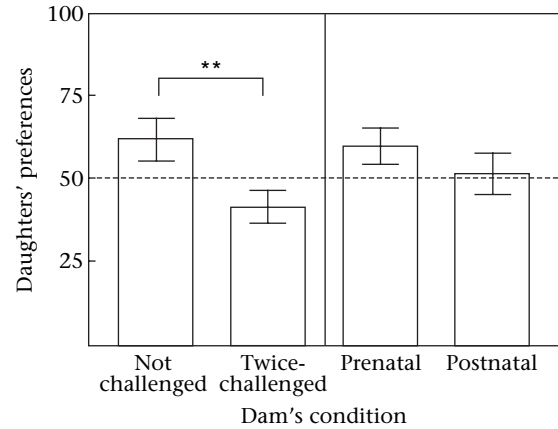
The observed difference in preference for mates between daughters of twice-challenged and not-challenged gerbil dams was as great as that between nominally socially monogamous prairie voles, *Microtus ochogoster*, and promiscuous montane voles, *Microtus montanus*, observed in apparatus similar to that used here (Carter et al. 1995; Insel & Young 2001; Young & Wang 2004). Differences in the conditions under which genetically similar females are reared may have an effect on mate attachment as great as that attributed to phylogeny.

Results of statistical analyses suggest that the postnatal challenge posed to third litters that nursed while their dams were gestating their fourth litters accounted for more of the variance in daughters' phenotypes than did the prenatal challenge to third litters gestated by dams nursing their second litters. Stressing female rodents (for example, by overcrowding or restraint) is known to masculinize their female offspring (e.g. Marchlewska-Koj et al. 2003; Ward & Weisz 1984; Kinsley & Bridges 1988). However, daughters of twice-challenged gerbil dams in the present experiment did not show reproductive profiles typical of androgenized gerbil females. For example, although daughters of twice-challenged dams delivered female-biased litters and were not particularly attentive to their young, females androgenized in utero deliver male-biased litters and spend more time with their young than do females not androgenized in utero (rats: Kinsley & Bridges 1988; Kinsley 1990; gerbils: Clark et al. 1993; house mice, *Mus domesticus*: Vandenbergh & Huggett 1994).

Our failure to find significant interactions between effects of prenatal and postnatal challenges to dams on either their daughters' attachment to their mates or their fecundity indicates that observed effects were not a result of prenatal challenge to a dam affecting the postnatal care that she provided for her daughters (Francais et al. 2003). Differences either in maternal care given to daughters (Levine 1995; Moore 1995; Meaney 2001; Weaver et al. 2004) or in the quantity or composition of the milk daughters ingested (Roubertoux et al. 1990) are thus likely

explanations for observed effects of challenges to dams on their daughters' reproductive phenotypes when adult. In retrospect, it would have been wise to have monitored the growth of female pups in third litters from birth to weaning, in addition to ascertaining their weight at birth (Table 2), to look for direct evidence of differences in postnatal maternal investment by dams assigned to the four groups. We did not make such measurements, in part because we feared that too much disturbance of litters would result in their abandonment.

Variations in the development of offspring resulting from differences in the demands on a dam's resources while gestating and nursing her young are potential causes of phenotypic plasticity in all mammals that are sometimes simultaneously pregnant and nursing.

We observed profound effects of reproductive challenges to dams on their daughters' reproduction and behaviour in a relatively benign laboratory environment where dams had ad libitum access to food and were protected from thermal stress and risk of predation. Effects of reproductive challenges to mothers on their daughters' reproductive profiles might be greater in more challenging natural environments. Thus, the present results suggest that some of the variability in adult social organization and reproductive behaviour routinely observed in rodents in both laboratory and field (e.g. Bernado 1996; Mousseau & Fox 1998; Crabbe et al. 1999; West-Eberhard 2003) may be a consequence of past conflicts between successive litters for the resources that their dam provided while caring for them.

References

Bernado, J. 1996. Maternal effects in animal ecology. *American Zoologist*, **36**, 83–105.

Carter, C. S., DeVries, A. C. & Getz, L. L. 1995. Physiological substrates of mammalian monogamy: the prairie vole model. *Neuroscience and Biobehavioral Review*, **19**, 303–314.

Clark, M. M. & Galef, B. G., Jr. 1995a A gerbil dam's intrauterine position affects the sex ratio of litters she gestates. *Physiology & Behavior*, **57**, 297–299.

Clark, M. M. & Galef, B. G., Jr. 1995b Prenatal influences on reproductive life history strategies. *Trends in Ecology and Evolution*, **10**, 151–153.

Clark, M. M. & Galef, B. G., Jr. 1998 Effects of intrauterine position on the behavior and genital morphology of litter-bearing rodents. *Developmental Neuropsychology*, **14**, 197–211.

Clark, M. M., Spencer, C. A. & Galef, B. G., Jr. 1986 Reproductive life-history correlates of early and late sexual maturation in female Mongolian gerbils (*Meriones unguiculatus*). *Animal Behaviour*, **34**, 551–560.

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., Karpiuk, P. & Galef, B. G., Jr. 1993 Hormonally mediated inheritance of acquired characteristics in Mongolian gerbils. *Nature*, **364**, 712.

Clark, M. M., Moghaddas, M. & Galef, B. G., Jr. 2002 Age at first mating affects parental effort and fecundity of female Mongolian gerbils. *Animal Behaviour*, **63**, 1129–1134.

Crabbe, J. C., Wahlsten, D. & Dudek, B. C. 1999. Genetics of mouse behavior: interactions with laboratory environment. *Science*, **284**, 1670–1671.

Elwood, R. W. & Broom, D. M. 1978. The influence of litter size and parental behaviour on the development of Mongolian gerbil pups. *Animal Behaviour*, **26**, 438–454.

Francais, D. D., Szegda, K., Campbell, G., Martin, W. D. & Insel, T. R. 2003. Epigenetic sources of behavioural differences in mice. *Nature Neuroscience*, **6**, 445–446.

Gromov, V. S. 1992. Behavioural ecology of Mongolian gerbils in Central Asia. In: *Behaviour and Communication of Mammals* (Ed. by V. E. Sokolov), pp. 76–114. Moscow: NAUKA.

Insel, T. R. & Young, L. J. 2001. The neurobiology of attachment. *Nature Review Neuroscience*, **2**, 129–136.

Kinsley, C. H. 1990. Prenatal and postnatal influences on parental behavior in rodents. In: *Mammalian Parenting: Biochemical, Neurobiological and Behavioral Determinants* (Ed. by N. A. Krasnegor & R. S. Bridges), pp. 347–371. Oxford: Oxford University Press.

Kinsley, C. H. & Bridges, R. S. 1988. Prenatal stress and maternal behavior in intact virgin rats: response latencies are decreased in males and increased in females. *Hormones and Behavior*, **22**, 76–89.

Leont'ev, A. N. 1954. K. ekologii kogtistoi, peschanki v Buryat Mongol'skoi (Ecology of the clawed gerbil in Buryat Mongolia). *Izvestiya Irkutskogo Osudarstvennyi Nauchno-Isledovatel'skogo Provitochumnogo Insituta Sibiri ii Dal'nago Vostoka*, **12**, 137–149.

Levine, S. 1995. Maternal behavior as a mediator of pup adrenocortical function. *Annals of the New York Academy of Sciences*, **746**, 260–275.

Marchlewska-Koj, A., Kruczek, M., Kapusta, J. & Pochron, E. 2003. Prenatal stress affects the rate of sexual maturation and attractiveness in bank voles. *Physiology & Behavior*, **79**, 305–310.

Martinez-Gomez, M., Juzarez, M., Distel, H. & Hudson, R. 2004. Overlapping litters and reproductive performance in domestic rabbit. *Physiology & Behavior*, **82**, 629–636.

Meaney, M. J. 2001. Maternal care, gene expression and the transmission of individual differences in stress reactivity across generations. *Annual Review of Neuroscience*, **24**, 1161–1192.

Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford: Oxford University Press.

Moore, C. 1995. Maternal contributions to mammalian reproductive development and the divergence of males and females. *Advances in the Study of Behavior*, **24**, 47–118.

Mousseau, T. A. & Fox, C. W. 1998. *Maternal Effects as Adaptations*. Oxford: Oxford University Press.

Norris, M. L. & Adams, C. E. 1981. Mating postpartum and length of gestation in the Mongolian gerbil (*Meriones unguiculatus*). *Laboratory Animals*, **15**, 189–191.

Ochirov, Yu. D. & Bashanov, K. A. 1975. *Mlekopitauschie Tuvy* (*Mammals of Tuva*). Kyzyl (Tuva, USSR): Tuva Publications (in Russian).

Roubertoux, P. L., Nosten-Bertrand, M. & Carlier, M. 1990. Additive and interactive effects between genotype and maternal environments, concepts and facts. *Advances in the Study of Behavior*, **19**, 205–247.

Ryan, B. C. & Vandenbergh, J. 2002. Intrauterine position effects. *Neuroscience and Biobehavioral Review*, **26**, 665–678.

vom Saal, F. S. 1981. Variation in phenotype due to random intrauterine positioning of male and female fetuses in rodents. *Journal of Reproduction and Fertility*, **52**, 633–650.

vom Saal, F. S., Clark, M. M., Galef, B. G., Jr, Drickamer, L. & Vandenbergh, J. 1999. The intrauterine position (IUP) phenomenon. In: *Encyclopedia of Reproduction. Vol. 2* (Ed. by E. Knobil & J. D. Neill), pp. 893–900. San Diego: Academic Press.

Vandenbergh, J. G. & Huggett, C. L. 1994. Mother's prior intrauterine position affects the sex ratio of her offspring in house mice. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 11055–11059.

Ward, I. L. & Weisz, J. 1984. Differential effects of maternal stress on circulating levels of corticosterone, progesterone and testosterone in male and female rat fetuses and their mothers. *Endocrinology*, **114**, 1635–1644.

Weaver, I. C. G., Cervoni, N., Champagne, F. A., D'Alessio, A. C., Sharma, S., Seckl, J. R., Dymov, S., Szyf, M. & Meaney, J. J. 2004. Epigenetic programming by maternal behaviour. *Nature Neuroscience*, **7**, 847–854.

West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

Woodside, B., Wilson, R., Chee, P. & Leon, M. 1981. Resource partitioning during reproduction in the Norway rat. *Science*, **211**, 76–77.

Young, L. J. & Wang, Z. 2004. The neurobiology of pair bonding. *Nature Neuroscience*, **7**, 1048–1054.