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Further evidence of sex-biased maternal investment by Mongolian gerbil dams

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> (Received 26 July 1990; initial acceptance 11 September 1990; final acceptance 28 November 1990; MS. number: As-734)

There is theoretical reason to expect that in polygynous species, as a consequence of competition between males for access to females, (1) a given increment in parental investment (Trivers 1972) will have a greater effect on the fitness of males than of females and (2) parents will make greater investment in individual sons than in individual daughters (Trivers & Willard 1973; Clutton-Brock & Albon 1982; Clutton-Brock & Iason 1986).

Unfortunately, as Clutton-Brock & Albon (1982), Clutton-Brock & Iason (1986) and Hrdy (1987) each have made clear, in their respective reviews of relevant literature, predictions about sexbiased parental investment are difficult to test empirically because of the lack of data describing either the fitness costs to parents of rearing young of each sex or the relative effects of a given amount of parental investment on the survival and reproduction of offspring of each sex.

In a recent paper (Clark et al. 1990), we presented evidence that female Mongolian gerbils, *Meriones unguiculatus*, exhibit a greater loss in reproductive potential after rearing sons than after rearing daughters. Here, we examine effects of reductions in maternal investment on rates of growth of nursing male and female Mongolian gerbil pups. On theoretical grounds (Clutton-Brock & Iason 1986), one would expect male pups to be more vulnerable to parental deprivation than their sisters.

Our subjects were 41 litters of gerbils, born to primiparous females descended from breeding stock acquired from Tumblebrook Farms (Brookfield, Massachusetts). On the day of birth, each litter was culled to two male and two female pups and each pup was toe clipped for individual recognition. Because of the demands of our experimental design, we used only those 30 litters that, on day 5 postpartum, had all four pups both alive and (to exclude runts) within a range of 0.5 g in weight. Three female and two male pups, one in each of five litters, died between days I and 5 postpartum.

On day 5 postpartum, we randomly assigned each litter to one of three groups (10 litters/group) that experienced either 0, 2 or 4 h/day of separation from their dams. Within each litter in 2 h/day and 4 h/day conditions, we randomly assigned one male and one female pup to the experimental condition and the remaining male and female pup to the control condition.

On each of days 5–15 postpartum, both control pups in litters assigned to 2-h and 4-h conditions and all four pups in litters assigned to the 0-h condition were removed from their home cages, weighed and immediately returned to their respective dams. On each of days 5–15 postpartum, the two experimental pups in each litter in 2-h and 4-h conditions were removed from their home cages, were weighed and, before being returned to their respective home cages, were placed together for either 2 or 4 h in a Plexiglas container floating in a constant temperature bath maintained at 28°C. We then calculated the mean percentage change in body weight of each pup across the 10 days of the experiment.

Both male and female control subjects in litters assigned to 2-h and 4-h groups gained more weight during the 10 days of the experiment than did subjects of the same sex in the 0-h separation group (Fig. 1). On the often-made (Clutton-Brock & Iason 1986), though obviously questionable, assumption that the body weights of juveniles are positively correlated with their survival, the excess weight gain exhibited by control subjects in 2-h and 4-h conditions, relative to subjects of the same sex in the 0-h condition, indicates that pups in experimental conditions lost parental investment in Trivers' (1972, page 249) sense of that which 'increases the offspring's chance of surviving while decreasing the parent's ability to invest in other offspring'.

Analysis $(2 \times 2 \text{ ANOVA})$ of the weight loss of separated male and female pups (those in the experimental conditions) relative to their same sex littermates in the control condition showed that hours of separation $(F=66\cdot09, df=1,36, P<0\cdot001)$ and sex of subjects $(F=4\cdot78, df=1,36, P<0\cdot03)$, but not their interaction $(F=0\cdot11, df=1,36, Ns)$, significantly affected the difference in weight gain between control and experimental subjects.

0003-3472/91/070161+02 \$03.00/0

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Figure 1. Mean $(\pm sE)$ percentage weight gain during the 10 days of the experiment by control (\triangle) and experimental (\blacksquare) male (a) and female (b) subjects under separation conditions of 0 h/day, 2 h/day and 4 h/day.

Experimental male pups exhibited significantly smaller mean percentage increases in body weight, relative to their same-sex, control siblings, than did experimental female pups relative to their same-sex, control siblings. Within-litter, within-sex matched *t*tests (Wike 1985) revealed a statistically reliable greater impact on male than on female pups in both the 2-h and 4-h conditions of separation (both ts > 2.09, df = 9, both Ps < 0.032).

Our previous results (Clark et al. 1990) indicated that gerbil dams invest more in their sons than in their daughters. The present data indicate that, in Mongolian gerbils, loss of a fixed period of maternal attention has greater impact on growth of sons than on growth of daughters (see also Labov et al. 1986). Taken together, the results of our two experiments are consistent with Clutton-Brock & Albon's (1983) and Clutton-Brock & Iason's (1986) predictions on theoretical grounds that: (1) parents will make greater investment in individual sons than in individual daughters (Clark et al. 1990) and (2) a given amount of parental investment will have greater effect on a son than on a daughter.

We gratefully acknowledge support from the Natural Science and Engineering Research Council of Canada to both M.M.C. and B.G.G., Jr and from the McMaster University Research Council to B.G.G., Jr.

REFERENCES

- Clark, M. M., Bone, S. & Galef, B. G., Jr. 1990. Evidence of sex-biased maternal investment by Mongolian gerbils. *Anim. Behav.*, **39**, 735–744.
- Clutton-Brock, T. H. & Albon, S. D. 1982. Parental investment in male and female offspring in mammals. In: *Current Problems in Sociobiology* (Ed. by King's College Sociobiology Group), pp. 223-247. Cambridge: Cambridge University Press.
- Clutton-Brock, T. H. & Iason, G. R. T. 1986. Sex ratio variation in mammals. Q. Rev. Biol., 61, 339-374.
- Hrdy, S. B. 1987. Sex-biased parental investment among primate and other mammals: a critical evaluation of the Trivers-Willard hypothesis. In: *Child Abuse and Neglect: Biosocial Dimensions* (Ed. by R. Gelles & J. Lancaster), pp. 97-147. New York: Aldine.
- Labov, J. B., Huck, U. W., Vaswani, P. & Lisk, R. D. 1986. Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters. *Behav. Ecol. Sociobiol.*, 18, 241–249.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.
- Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90–92.
- Wike, E. 1985. Numbers: a Primer of Data Analysis. Columbus, Ohio: Merill.