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Evidence of sex-biased postnatal maternal investment by Mongolian gerbils

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Abstract. Three experiments were undertaken examining the relative costs to female Mongolian gerbils, *Meriones unguiculatus*, of rearing four male or four female pups from birth to weaning. In experiment 1, it was observed that gerbil dams rearing all-male litters were almost twice as likely as gerbil dams rearing all-female litters to be found: (1) with all their young in the nest throughout a 20-min observation period; and (2) with one or more pups attached to their nipples. In experiment 2, (1) dams rearing all-male litters delivered significantly fewer young as a consequence of impregnation during postpartum oestrus than did dams rearing all-female litters and (2) dams rearing all-male litters exhibited both significantly greater periods of vaginal closure (preventing copulation) and significantly greater inter-litter intervals than did dams rearing all-female litters. In experiment 3, it was found that vaginal closure also provides an index of whether a gerbil dam will transfer milk to her pups. Consequently, the greater durations of vaginal closure observed in dams rearing all-male litters than in dams rearing all-female litters (experiment 2) suggest a longer period of milk transfer from dams to their male than to their female young before weaning. The data were interpreted as consistent with the hypothesis that rearing male pups was more costly to gerbil dams than was rearing female pups. Difficulties in determining the relative cost to dams of rearing male and female young were discussed.

Sex-biased parental investment is expected to occur whenever variation in reproductive success is greater for members of one sex than for members of the other (Trivers & Willard 1973). Such sex-biased parental investment might be evidenced by parental manipulation of the sex ratio of offspring prior to birth (for review, see Clutton-Brock & Iason 1986), by assignment of different amounts of parental investment to sons and daughters during a postnatal period when young are dependent on parental sustenance (for reviews, see Clutton-Brock & Albon 1982; Hrdy 1987), or by differences in the behaviour of parents towards sons and daughters after they have matured (for review, see Clutton-Brock & Albon 1982). We shall be concerned below with measurement of female Mongolian gerbils', *Meriones unguiculatus*, relative investments in their male and female offspring during the period from birth to weaning.

In polygynous species, including many rodents, as a result of competition among males for access to females, there is reason to expect greater variability in male than in female reproductive success. Consequently, in polygynous species, one would expect to find greater parental investment in sons than in daughters where parental investment is defined as 'anything done by the parent for the offspring that increases the offspring's chance of surviving while decreasing the parent's ability to invest in other offspring' (Trivers 1972, page 249).

Unfortunately, as Clutton-Brock & Albon (1982), Clutton-Brock & Iason (1986) and Hrdy (1987) have each made clear in their reviews of relevant data, predictions about sex-biased parental investment are difficult to test empirically because of the lack of data describing either the relative effects of a given amount of parental investment on the survival of sons and daughters or the relative fitness costs to parents of rearing male or female offspring. Although there is considerable evidence, especially in mammals, that infant sons and daughters are treated differently by their dams (Moore & Morelli 1979; Clutton-Brock et al. 1982; Clark & Galef 1989), measurement of changes in reproductive potential resulting from rearing sons and daughters is rare as is evidence of enhanced survival of young as a result of increased parental attention.

The three experiments reported below were undertaken first, to describe differences in the maternal care that female Mongolian gerbils direct toward all-male and all-female litters (experiments 1 and 3), and second, to look for evidence of differences in the reproductive potential of female gerbils (i.e. their probability of producing progeny) after rearing male or female young (experiment 2).

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EXPERIMENT 1

Observation of differences in the parental behaviour that gerbil dams direct toward their young of each sex can provide only indirect evidence that dams are investing differently in sons and daughters. Such observations cannot show either that the survival of the sex receiving greater maternal attention is increased or that the future reproductive potential of dams providing greater maternal care is decreased. On the other hand, if there were no differences in the behaviour dams direct toward their young of each sex, then it is not obvious how dams could be investing differently in sons and daughters postnatally.

We have reported previously (Clark et al. 1989) that gerbil dams, like Norway rat, *Rattus norvegicus*, dams (Moore & Morelli 1979; Clark & Galef 1989), more often lick their sons' anogenital regions than their daughters'. It is, however, difficult to argue that anogenital licking of pups is costly to dams. If licking does not reduce a dam's subsequent reproductive potential, then amount of anogenital licking is not an index of parental investment (Trivers 1972).

In this experiment, we sampled a number of potentially energetically costly behaviours exhibited by lactating gerbils rearing either four male or four female pups. Our goal was to determine whether there were any observable differences in the amount of attention females directed toward their young of each sex that might suggest that they were, in fact, investing differently in sons that in daughters.

Methods

Subjects

Thirty-two female Mongolian gerbils, born in the McMaster vivarium to breeding stock acquired from Tumblebrook Farm (Brookfield, Massachusetts), and each female's first litter served as subjects.

Because (1) there are marked differences in the patterns of maternal care and reproductive behaviour exhibited by female gerbils correlated with their respective ages at vaginal introitus (Clark et al. 1986b) and (2) we were looking for what might be relatively small effects on maternal and reproductive behavour, we reduced uncontrolled variability in the behaviour of our subjects by selecting dams to participate in the experiment on the basis of their ages at vaginal introitus. All 32 dams in the present experiment had matured early, i.e. all had exhibited vaginal introitus before reaching 25 days of age (Clark et al. 1986b). We used early-maturing rather than late-maturing females as dams because the former are both easier to mate and more fecund than the latter (Clark et al. 1986a, 1986b).

Breeding and maintenance

At 90 days of age, each adult female subject was placed individually with a sexually proven, adult male gerbil born in the McMaster colony. The 32 breeding pairs were housed individually in polypropylene shoebox cages measuring 35 × 30 × 15 cm, with $\frac{1}{2}$-in (1·3-cm) hardware cloth lids and carpeted with a thin layer of wood-chip bedding (Betta-chips, Northeastern Products, Warrensburg, New York). They were fed Purina Rodent Laboratory Chow no. 5001 and water ad libitum in a single temperature- and humidity-controlled colony room on a 12:12 h light:dark cycle (light onset at 0500 hours).

Each breeding pair was examined daily at 1100 hours and, when a female was conspicuously pregnant (i.e. late in the second or early in the third week of pregnancy), her mate was removed from her cage.

On the day of birth of a litter (day 1 postpartum), each litter was culled to either four male ($N = 16$ litters) or four female ($N = 16$ litters) pups and each pup in each culled litter was toe clipped for permanent identification. Litters were weaned at day 30 postpartum.

Procedure

An observer, unaware of the gender of the pups a female was rearing, observed the behaviour of each dam for 20 min/day, between 1000 and 1400 hours, on each of days 5, 9, 13, 17 and 21 postpartum. Once every 10 s throughout each 20-min observation period (i.e. on 120 occasions), the observer recorded whether: (1) one or more pups were attached to their respective dam's nipples, (2) pups were in physical contact with their dam, but not sucking, (3) all of a dam's pups were gathered together in the nest, (4) the dam was away from her pups and active (e.g. exploring, digging, scratching, rearing or locomoting about the cage), or (5) the dam was away from her pups and inactive (e.g. sleeping or immobile).

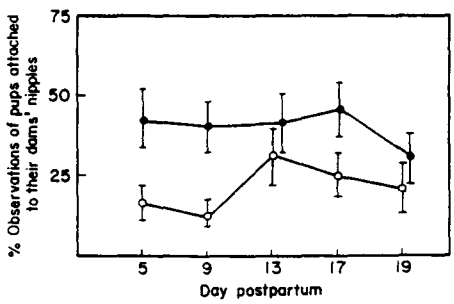

Figure 1. Mean percentage of 120 observations during which one or more pups in all-male (●) or all-female (○) litters were attached to the nipples of their respective dams. Vertical bars indicate ± 1 SE.

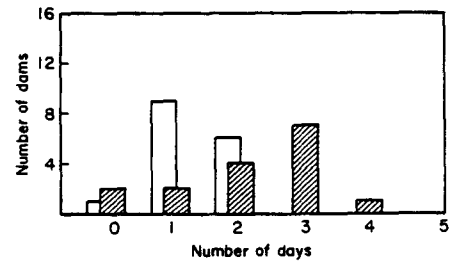

Figure 2. Number of dams rearing all-male (▨) and all-female (□) litters that had all four of their pups gathered together in the nest throughout 0, 1, 2, 3, 4 or 5 of the five 20-min periods of observation.

The observer also examined the vagina of each dam both on day 25 and day 30 postpartum to determine whether her vagina was open or closed. Vaginal closure was defined as a decrease in the size of the vaginal orifice and growth of vaginal membrane (Meckley & Ginther 1972, 1973).

Results

Maternal behaviour

The main results of experiment 1 are presented in Figs 1 and 2, where it can be seen that dams rearing all-male litters spent significantly more time suckling their young ($F_{1,15} = 11{\cdot}345$, $P < 0{\cdot}004$; Fig. 1) and had all their young gathered together in the nest throughout 20-min observation periods on significantly more days than did dams rearing all-female litters (Student's t-test, $t_{30} = 2{\cdot}66$, $P < 0{\cdot}01$; Fig. 2).

It is, of course, possible that these results reflected a greater propensity of male than of female gerbil pups to remain immobile or to return to the nest on their own. However, observation of the behaviour of dams in response to spontaneous movement of their 5-, 9- and 13-day-old young from the nest indicated that the observed greater probability of finding all-male than all-female litters in the nest was, in fact, a result of differences in dams' behaviour toward sons and daughters. Dams rearing all-female litters, one or more of whose young were out of the nest during an observation period ($N = 16$ dams), were observed to retrieve their displaced young to the nest before the end of that observation period with an average probability of 0·36. Dams rearing all-male litters whose young strayed ($N = 11$ dams) exhibited a mean probability of 0·64 of retrieving their young before the end of the observation period. Thus, dams rearing all-male litters were significantly more likely to recover strays during an observation period than were dams rearing all-female litters ($\chi^2 = 3{\cdot}24$, $df = 1$, $P < 0{\cdot}03$, one-tailed).

The observed differences in the behaviour of the dams were not the result of generalized differences in the activity levels of females rearing sons and daughters. Neither the percentage of time a dam was active (as opposed to inactive) while away from her pups ($F_{1,15} = 0{\cdot}60$, $P > 0{\cdot}10$) nor the percentage of time a female spent in contact with her pups, but not nursing them ($F_{1,15} = 0{\cdot}31$, $P > 0{\cdot}10$) differed between those dams rearing all-male and all-female litters.

Vaginal status of dams

Dams rearing all-male litters were less likely than were dams rearing all-female litters to have their vaginas open both on day 25 (1/16 versus 8/16) and on day 30 (9/16 versus 15/16) postpartum (Fisher's exact tests, $P < 0{\cdot}01$ in both cases).

Discussion

The results of experiment 1 provide clear evidence of differences in overt patterns of maternal care exhibited by female gerbils caring for male or female young during the period from birth to weaning. Whether these differences in maternal behaviour reflect true differences in maternal investment, in the sense of reducing females' future reproductive success (Trivers 1972), is examined in experiment 2.

Vaginal closure seals the vagina of female gerbils and would prevent intromission during any attempted copulation. The greater period of vaginal closure exhibited by dams rearing all-male rather than all-female litters is, therefore, a possible indication of reduced fecundity resulting from rearing male rather than female pups.

EXPERIMENT 2

Both in the laboratory and in natural circumstances, female Mongolian gerbils, like females of many other rodent species, enter into oestrus 12–48 h after delivery of a litter (Leont'ev 1954; Asdel 1964; Marston & Chang 1965). A female would have relatively little opportunity to recover from the effects of investment in one litter (litter A) before rearing a second litter (litter B) conceived in the postpartum oestrus associated with the birth of litter A. Therefore, one might expect to observe reduced reproductive potential resulting from a female's investment in litter A revealed most clearly in her reproductive performance with litter B, the litter conceived during the postpartum oestrus associated with the birth of litter A.

A female could compensate for a large investment in litter A in many different ways. For example, a female that was rearing a costly litter A could lower her probability of becoming pregnant during postpartum oestrus. She could reduce the cost of litter B, conceived during postpartum oestrus, either by reducing the size of litter B or by reducing the proportion of the more costly sex in litter B. She could reduce her total daily reproductive effort by delaying implantation of the eggs of litter B (Norris & Adams 1971, 1981). Experiment 2 was undertaken to determine whether we could detect effects of the sex of the members of the litter of pups a female was rearing (litter A) on her reproductive performance with a litter (litter B).

It is important to note that, in gerbils, blastocysts do not become implanted in the uterus for 7–10 days following copulation (Marston & Chang 1966; Norris & Adams 1971; Meckley & Ginther 1973). Consequently, there is opportunity for the cost of maintaining litter A to affect the reproductive behaviour exhibited by a female gestating litter B, a litter conceived during the postpartum oestrus associated with the birth of litter A.

Methods

Subjects

Thirty-four, early-maturing, female Mongolian gerbils, born and reared in the McMaster vivarium, and each female's first- and second-born litters served as subjects.

Breeding and maintenance

Dams were maintained and bred as described in the Methods section of experiment 1 except that a male was not removed from his mate's cage until 2 weeks following delivery of her first litter (Norris 1985).

Procedure

Cages of breeding pairs were examined daily at 1100 hours for the presence of litters. On the day of birth of a litter (day 1 postpartum), each litter was culled to either four male ($N=17$ litters) or four female ($N=17$ litters) pups. After culling, each dam was left to rear her four remaining offspring without disturbance, except as noted below.

Each dam was inspected daily from day 3 postpartum until her vagina closed and again from day 15 to day 45 postpartum to determine when her vagina reopened.

Results

The main results of experiment 2 are presented in Table I. The data were analysed with respect to the hypothesis that dams invested more in all-male litters than in all-female litters.

As can be seen in Table I, the mean size at birth of litters conceived during postpartum oestrus by dams rearing all-male litters was slightly, but not significantly, smaller than the mean size at birth of litters conceived during postpartum oestrus by dams rearing all-female litters (Student's $t_{27}=1{\cdot}11$, $P=0{\cdot}28$). However, simply looking at the number of pups brought to term in litters conceived during postpartum oestrus by those 29 dams that reared all-male or all-female litters and became pregnant in postpartum oestrus does not take into account the fact that dams rearing all-male litters were less likely to conceive during the postpartum oestrus than were dams rearing all-female litters (see Table I). To observe the full impact of rearing all-male and all-female litters on the reproductive success associated with postpartum oestrus, we compared the mean number of young delivered by all 17 dams

Table I. Reproductive performance of Mongolian gerbil dams assigned to rear all-male or all-female litters

Litter composition	All-male	All female
N	17	17
Mean size of first litter (A)	6·4 ± 0·4	6·6 ± 0·4
Mean % males in first litter (A)	64·5 ± 5·5	39·7 ± 3·7
Mean duration of vaginal closure (days)	19·4 ± 1·1	15·6 ± 0·8
Mean number of pups delivered in litter (B) by all 17 females	4·5 ± 0·7	6·1 ± 0·4
% Females pregnant in postpartum mating (*N*)	76·5 (13)	94·1 (16)
Mean inter-birth interval (days)*	38·3 ± 1·4	34·5 ± 1·0
Mean size at birth of litter (B) conceived in postpartum mating*	5·8 ± 0·5	6·5 ± 0·4
Mean % males in second litter (B)*	51·8 ± 5·9	43·3 ± 4·5

Mean values are ± 1 SE.
*Cell entries refer only to those 29 females giving birth to a litter (B) conceived in postpartum oestrus.

rearing all-male litters with the mean number of young delivered by all 17 dams rearing all-female litters and found a 26% decrease in fecundity for dams rearing all-male litters (median test, $\chi^2 = 4{\cdot}25$, $df = 1$, $P < 0{\cdot}05$).

Inter-birth interval for the 29 females rearing two litters also varied significantly as a function of the sex of the litter a female was rearing. Mothers rearing all-female litters had significantly shorter mean inter-birth intervals ($t_{27} = 2{\cdot}18$, $P < 0{\cdot}05$). Again, looking at the inter-birth intervals of only those females that gave birth to two litters ignores the fact that a greater number of dams rearing all-male litters than of dams rearing all-female litters did not give birth to a second litter and, therefore, exhibited what were, for statistical purposes, effectively infinite inter-birth intervals. Median inter-litter intervals for all 17 of the dams rearing all-male litters was 41 days and for the 17 dams rearing all-female litters was 33 days (median test, $\chi^2 = 5{\cdot}6$, $df = 1$, $P < 0{\cdot}02$), a 24% increase in median inter-birth interval resulting from rearing male rather than female pups.

Dams rearing all-female litters also exhibited shorter durations of vaginal closure than did females rearing all-male litters ($t_{32} = 2{\cdot}25$, $P < 0{\cdot}03$; Table I). The difference between dams rearing all-male and all-female litters in duration of vaginal closure remained significant even when we analysed data from only those 29 females that conceived during postpartum oestrus and were, therefore, both pregnant and lactating following birth of their first litters ($t_{27} > 1{\cdot}88$, $P < 0{\cdot}05$, one-tailed test). To the extent that duration of vaginal closure is an index of maternal investment or maternal care in female gerbils (see experiment 3), those females raising all-male litters were providing more investment in, or care for, their litters than were those females raising all-female litters.

The sex ratios of litters conceived in postpartum oestrus by dams rearing all-male litters were male biased and those of females rearing all-female litters were female biased, but the difference in mean sex ratio was not statistically significant ($t_{27} = 1{\cdot}13$, $P > 0{\cdot}25$).

Discussion

Several measures of differences in the reproductive performance during postpartum oestrus of dams rearing all-male or all-female litters were consistent with the hypothesis that rearing male gerbil pups had a greater deleterious effect on dams' reproductive potential than did rearing female gerbil pups. Gerbil dams rearing all-male litters: (1) had significantly fewer young as a consequence of postpartum oestrus; and (2) exhibited significantly longer mean and median inter-birth intervals than did dams rearing all-female litters. The non-significant finding that dams rearing all-male litters tended to give birth to male-biased litters, while dams rearing all-female litters tended to give birth to female-biased litters, was the sole finding in experiment 2 that would not be predicted on the hypothesis that male gerbil pups are more costly to rear that their sister.

EXPERIMENT 3

One of the major impediments to measuring either the amount or duration of postpartum, maternal care by mammals is the absence of a simple, non-intrusive index of milk transfer from mother to young around the time of weaning. Young rodents

begin to eat solid food long before weaning is completed (Galef 1979), so pup weight gain is not necessarily an index of milk flow. On the other hand, observation of nipple attachment by juveniles is not necessarily indicative of milk transfer because juvenile mammals may continue to attach to their dam's nipples even when milk flow from their dam is absent or greatly reduced (Williams et al. 1979, 1980).

As noted above, female Mongolian gerbils are unusual (though not unique) in that the vaginas of nursing females seal some 6 days after parturition and remain sealed throughout much of lactation (Meckley & Ginther 1972, 1973). Meckley & Ginther's (1973) observation that removal of a litter from a lactating gerbil dam accelerated reopening of her vagina led us to inquire as to whether vaginal closure might serve as an index of continued milk transfer by gerbil dams to their young.

Methods

Subjects

Sixteen, early-maturing, nulliparous, female Mongolian gerbils, born and reared in the McMaster vivarium, and their first litters of young, culled to two male and two female pups per litter on the day of their birth, served as subjects.

Breeding and maintenance

Conditions of breeding and maintenance throughout the experiment were those described in Methods of experiment 1.

Procedure

The experiment was conducted using eight pairs of dams as subjects. The two members of each pair were matched for date of parturition and were tested on the same day postpartum. The dam rearing one litter in each pair was selected because she had an open vagina on the day of testing (one dam on each of days 20, 24, 27 and 29; two dams on each of days 28 and 30); the dam rearing the other litter in each pair was selected because she had a sealed vagina on the day of testing.

To begin a test, the litters from each of a pair of dams were transferred from their respective home cages to deprivation cages where the members of each litter were maintained together for 4 h without food, but with ad libitum access to water. While the pups were being deprived of food, all food was removed from their respective home cages. At the end of the 4-h deprivation period, pups in each litter were weighed and returned to their dams. Pups were then left undisturbed for 2 h to suckle. Each pup was then reweighed to determine its change in weight during the 2-h period of interaction with its dam.

Data analysis

The mean weight change of the male and of the female members of each litter were used as individual data points in statistical tests.

Results and Discussion

The main results of experiment 3 are presented in Fig. 3. Both male and female pups returned to dams with sealed vaginas gained markedly more weight than did their counterparts returned to dams with open vaginas (Mann–Whitney *U*-tests, both $Us < 5$, both $Ps < 0{\cdot}001$).

This finding suggests that the vaginal status of a female gerbil provides a useful index of her likelihood of contributing milk to her young. Those female gerbils exhibiting relatively prolonged periods of vaginal closure should be those exhibiting relatively prolonged periods of milk delivery to their young.

An informal observation made in the course of conducting experiment 2 was consistent with the hypothesis that duration of vaginal closure is an index of duration of maternal investment in gerbils. On any theory of maternal investment, one would expect those females that were lactating and also pregnant with a litter conceived during postpartum oestrus to be willing to invest less in their nursing litter than those females that were only nursing and had not conceived during postpartum oestrus. Of the 34 females in experiment 2, five were lactating and 29 were both pregnant and lactating. The mean ($\pm$SE) duration of vaginal closure for lactating females was $29{\cdot}8 \pm 2{\cdot}9$ days and for females both pregnant and lactating was $23{\cdot}9 \pm 0{\cdot}8$ days. Such greater duration of vaginal closure in non-pregnant lactating females is consistent with the hypothesis that duration of vaginal closure provides an index of maternal investment in a nursing litter.

The finding in both experiments 1 and 2 that gerbil dams rearing all-male litters exhibited

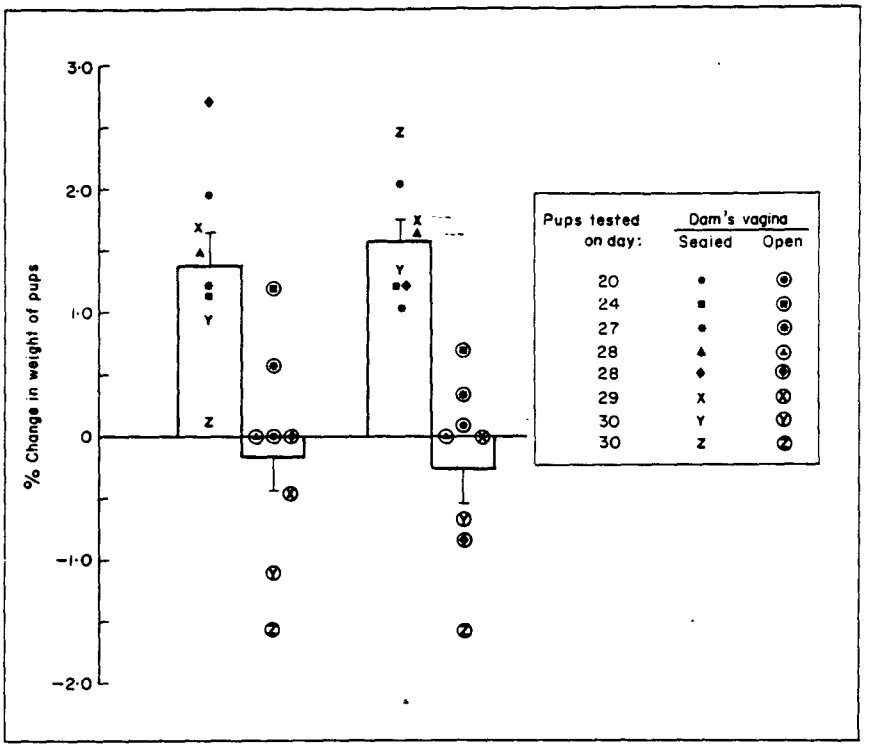

Figure 3. Mean percentage change in weight of male (left-hand pair of bars) and female (right-hand pair of bars) pups placed for 2 h with dams with open or sealed vaginas. Data points for pups from litters reared by dams assigned to the same pair have been given the same symbol.

greater durations of vaginal closure than did gerbil dams rearing all-female litters, taken together with the finding in the present experiment that the period of vaginal closure in postpartum gerbils corresponds to the period of milk delivery to young, suggests that male gerbil pups receive milk from their dams for a longer period of time than do female gerbil pups. The observation in experiment 1 that male pups were more likely to be found attached to their dams' nipples than were female pups also suggests greater milk flow from gerbil dams to their male than to their female offspring. It surprised us, therefore, to find no difference in the weights of all-male and all-female litters at 25 days of age (all-male litters: $(\bar{X} \pm \text{SE} = 76{\cdot}1 \pm 5{\cdot}3$ g; all-female litters: $\bar{X} \pm 75{\cdot}5 \pm 4{\cdot}9$ g). The failure to find differences in weights of male and female gerbil pups of weaning age is, however, consistent with previous observations (Clark & Galef 1980). The possibilities that male gerbil pups have higher basal metabolism rates than females, are more active than females, are less willing to eat solid food than females, or do more non-nutritive sucking than females need to be examined (see also Mendl & Paul 1989). Of course, even if male gerbil pups do receive more milk from their dams than do female gerbil pups, that does not mean that greater milk flow to male than to female pups was the cause of the reduced reproductive potential observed in dams rearing all-male litters in experiment 2.

GENERAL DISCUSSION

The results of the present series of experiments are consistent with the hypothesis that gerbil dams make a greater investment in their male than in their female offspring. (1) Direct observation of the behaviour of dams rearing all-male and all-female litters revealed that dams in the former condition nursed their young more frequently than did dams

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