Nonrandom Sex Composition of Gerbil, Mouse, and Hamster Litters Before and After Birth

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Examining data describing the sex composition of 1074 Caesarean-delivered litters of house mice, 253 Caesarean-delivered and 265 vaginally delivered litters of Mongolian gerbils, and 854 vaginally delivered litters of golden hamsters, we determined whether segregation of sexes between uterine horns and correlations between litter size and litter sex ratio were present in each of the three rodent species studied. Although significant deviations from expected distributions of male and female fetuses were found, these deviations from chance were not the same in any two of the three species examined. Analyses also indicated that the correlation between litter size and litter sex ratio that Huck, Seger, and Lisk (1990) found in vaginally delivered infant hamsters is present in vaginally delivered infant Mongolian gerbils, but not in their Caesarean-delivered colony mates. In gerbils, and perhaps hamsters as well, the correlation between litter size and litter sex ratio appears to be a result of sex-biased perinatal mortality correlated with litter size rather than of sex-biased conception correlated with litter size.

In all litter-bearing rodent species examined to date (e.g., mice, rats, hamsters and gerbils), the intrauterine locations of both male and female fetuses, relative to fetuses of opposite sex, have been found to be correlated with adult physiological, morphological, and behavioral characteristics (Clark & Galef, 1988; Clemens, Gladue, & Coniglio, 1978; vom Saal & Bronson, 1980a; Vomachka & Lisk, 1986). For example, female house mice (*Mus musculus*) that developed in intrauterine

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locations between two male fetuses attained puberty at later ages, had longer estrous cycles, were less fecund, and were both more aggressive towards and less sexually attractive to male house mice than were female mice that developed in intrauterine locations adjacent to no males (vom Saal, 1981, 1989a,b; vom Saal & Bronson, 1978, 1980a,b; vom Saal & Moyer, 1985; vom Saal, Pryor, & Bronson, 1981). Similarly, adult female Mongolian gerbils (*Meriones unguiculatus*) that as fetuses occupied intrauterine locations adjacent to one or two males, as adults exhibited more aggression, delayed puberty, reduced lifetime fecundity, and enhanced maternal behavior relative to females that matured in intrauterine locations distant from males (Clark & Galef, 1988; Clark, Spencer, & Galef, 1986a,b).

Correlates of intrauterine location with adult characteristics have been found in male as well as in female rodents. For example, those male gerbils that as fetuses resided in intrauterine locations adjacent to no females, as adults both scent marked more frequently and copulated more vigorously than did those male gerbils that *in utero* developed between two female fetuses (Clark, Malenfant, Winter, & Galef, 1990). Similar correlations between intrauterine location and copulatory pattern have been found in male house mice (vom Saal, Grant, McMullin, & Laves, 1983).

The probability that a fetus will develop adjacent to 0, 1, or 2 fetuses of the opposite sex is determined by four parameters: (a) the sex ratio, and (b) the size of the litter of which it is a member, and (c) the distribution of that litter's male and female siblings both within, and (d) between uterine horns. For example, as litter size increases, the probability that a fetus will be at the end of a line of pups in a uterine horn decreases. Consequently, the proportion of fetuses that are between either two male or female siblings increases with increasing litter size. Similarly, as the proportion of males in a litter rises, the probability of a fetus occupying an intrauterine location adjacent to no female fetuses increases as does the probability of a fetus occupying an intrauterine location adjacent to one or two male fetuses.

Recent papers provide evidence of nonrandom distribution of male and female fetuses both within and across litters in hamsters and gerbils. Clark and Galef (1990) found that female Mongolian gerbils tended to bear sexually segregated litters, with male fetuses gathered in the right uterine horn and female fetuses in the left. Consequently, both male and female gerbil fetuses were less likely to mature adjacent to fetuses of the other sex than one would expect if male and female fetuses had been randomly distributed across uterine horns (Clark & Galef, 1990).

Huck, Seger, and Lisk (1990) reported a positive correlation between litter size and the proportion of females in litters of golden hamsters (*Mesocricetus auratus*) that were examined within 8 hr of vaginal delivery. Presumably, though no one has looked, as the proportion of males in a hamster litter decreased from .70 (litters of 3) to .37 (litters of 18), the frequencies with which both male and female fetuses matured adjacent to either 1 or 2 female fetuses increased, while the probability that male or female fetuses developed adjacent to either 1 or 2 male fetuses decreased.

Vom Saal (1981) examined the intrauterine positions of Caesarean-delivered mouse fetuses and found no deviations from the proportions of females developing adjacent to 0, 1, or 2 males that would be expected on the hypothesis that male and female fetuses were randomly distributed within uterine horns. Vom Saal (1981) concluded that the intrauterine distribution of male and female mouse fetuses is random. Of course, other tests for randomness in distribution of mouse fetuses might have produced different results.

In the present article, two related issues were addressed: First we determined whether the positive correlation between litter size and proportion of females in litters of golden hamsters, described by Huck et al. (1990), and the sexual segregation of Mongolian gerbil fetuses, described by Clark and Galef (1990), generalize to other rodent species. In particular, we determined whether: (a) there was segregation of male and female fetuses in the left and right uterine horns of female house mice (as in female gerbils) and (b) mouse and gerbil litters (like golden hamster litters) exhibit systematic changes in sex ratio as a function of litter size. We subjected: (a) data from litters of house mice to analyses used by Clark and Galef (1990) to demonstrate sexual segregation of fetuses in left and right uterine horns of Mongolian gerbils and (b) data from litters of both house mice and gerbils to analyses used by Huck et al. (1990) to demonstrate correlations between litter sex ratio and litter size in golden hamsters.

Second, we asked whether statistical descriptions of the distribution of the sexes of litter members in the hours following vaginal delivery provide an accurate picture of the distribution of sexes in litter members on the day preceding birth (determined following Caesarian section). In particular, we determined whether litter sex ratios, variances in litter sex ratios, and the relationship of litter sizes to litter sex ratios in Mongolian gerbils were similar on the last day of gestation and the first day following vaginal delivery.

Ideally, we would have performed all analyses on all three subject species. Unfortunately, without access to sufficient data describing either the intrauterine positions of hamster fetuses or the postpartum sex ratios of mouse litters, this was not possible. By calling attention to biologically significant questions that can be answered with descriptive data from breeding programs, we hope to encourage those who either breed rodents or Caesarean deliver rodents as part of their normal research to keep records that, 3 to 5 years from now, will permit comparative analyses more comprehensive than those possible today.

Methods

Subjects

Subjects were 1074 litters of house mice (*Mus musculus*) (Caesarean-delivered, vom Saal's laboratory) and 253 litters of Mongolian gerbils (*Meriones unguiculatus*) (Caesarean-delivered, Clark's laboratory) that had served as subjects in the course of vom Saal's and Clark's respective investigations of uterine position effects on circulating levels of fetal hormones and fetal development. A further 265 litters of vaginally delivered Mongolian gerbils, examined in Clark's laboratory during studies of reproductive life histories of gerbils (Clark, Spencer, & Galef, 1986b) and 854 litters of vaginally delivered golden hamsters (*Mesocricetus auratus*), used by Huck et al. (1990) to examine effects of time of mating on litter sex ratios, also provided data for analysis.

Table 1

Mean Percent and Number of Male Fetuses in Left and Right Uterine Horns of Caesarian-Delivered Gerbils and Mice

		Mean percent males			Mean number of pups	
	N	left horn	right horn	litters	left horn	right horn
Gerbils[+]	253	41.8 ± 2.0	55.0 ± 2.0	49.9 ± 1.3	3.3 ± 0.1	3.2 ± 0.1
Mice	1074	52.4 ± 0.7	52.3 ± 0.7	52.4 ± 0.5	5.6 ± 0.1	6.0 ± 0.1

[+] From Clark & Galef (1990) Table 1.

N = number of litters.

Procedure

Procedures used to breed, maintain, and Caesarean deliver subjects in the present study have been described in detail elsewhere (Clark & Galef, 1990; vom Saal, 1981). Most relevant to present purposes: (a) both mouse and gerbil fetuses were Caesarean delivered late in pregnancy (mice 19 days and gerbils 24 days following copulation), (b) the sex of each fetus was determined using anogenital distance, (c) the number of both male and female fetuses in each uterine horn and in each litter were determined, and (d) the location of each fetus relative to adjacent fetuses of the same and opposite sex was recorded (vom Saal, 1989a, Clark & Galef, 1990).

Procedures used in breeding and maintaining vaginally delivered hamster and gerbil litters are described in detail in Huck et al. (1990) and Clark et al. (1986b), respectively. Each vaginally delivered litter of gerbils was examined within 15 hr of its birth and each vaginally delivered litter of hamsters within 8 hr of its birth. The anogenital distance of each gerbil and mouse pup was used to determine its gender.

Results and Discussion

Sexual Segregation in the Uterine Horns of Mice and Gerbils

As can be seen in Table 1, which shows the mean proportion of male fetuses in right and left uterine horns of both Caesarian-delivered gerbils and Caesarian-delivered house mice, there were differences between gerbils and mice both in the overall prenatal sex ratios of their respective litters and in the distribution of fetuses and of sexes across uterine horns. In mice, although significantly more fetuses were found in the right uterine horn than in the left ($t(1073) = 4.94$, $p < 0.01$), and there was a significant, overall male sex bias ($X^2 = 31.8$, $df = 1$, $p < 0.001$), there was no segregation of sexes in left and right uterine horns ($t(1073) = 0.41$, $p =$ n.s.).

In Caesarian-delivered gerbils, although there were equal numbers of pups in the two uterine horns ($t(252) = 0.67$, $p =$ n.s.) and the overall proportion of male fetuses did not differ significantly from 0.50 ($X^2 = 0.07$, $df = 1$, $p =$ n.s.), there was significant segregation of sexes: Males predominated in the right uterine horn and females in the left ($t(252) = 4.88$, $p < 0.001$).

Table 2

The Proportion of 1,635 Male Gerbil and of 12,450 Male Mouse Fetuses in Right and Left Uterine Horns Developing Adjacent to 0, 1, or 2 Female Fetuses

	Uterine horn	0	1	2
Gerbils⁺	Left	.30	.55	.14
	Right	.50	.41	.09
Mice	Left	.36	.49	.15
	Right	.38	.48	.13

⁺ From Clark & Galef (1990) Table 2.

As can be seen in Table 2, which shows the proportion of male gerbil and male mouse fetuses developing adjacent to 0, 1, or 2 female fetuses in left and right uterine horns, in gerbils (which showed uterine segregation of sexes), the left uterine horn produced a different distribution of male fetuses developing adjacent to 0, 1, and 2 female fetuses than did the right uterine horn ($X^2 = 31.0$, $df = 2$, $p < 0.0001$). In the right uterine horn of gerbils, where male fetuses were more frequent than female fetuses, 0F males were more common and 2F males less common than in the left uterine horn, where female fetuses were more frequent than male fetuses. In mice (which did not show uterine segregation of sexes), no differences were found between right and left uterine horns in the intrauterine positions of male fetuses relative to female fetuses ($X^2 = 4.62$, $df = 2$, $p =$ n.s.).

Relationships between Litter Size and Litter Sex Ratio in Mice, Hamsters, and Gerbils

Huck et al. (1990) have reported that, on the day of vaginal delivery, although the overall sex ratio of hamster litters did not depart from 0.50 ($X^2 = 0.00$, $df = 1$, $p =$ n.s.), larger litters had proportionally more females than did smaller litters (Spearman's *rho* = −0.96, $t(16) = 13.9$, $p < 0.001$). As can be seen in Table 3 (which shows the proportion of males in litters of hamsters, mice, and gerbils as a function of litter size on the day of delivery), vaginally delivered gerbils, like vaginally delivered hamsters, exhibited both an overall sex ratio not different from 0.50 ($X^2 = 0.60$, $df = 1$, $p =$ n.s.) and a larger proportion of females in large litters than in small ones (Spearman's *rho* = −0.89, $t(8) = 5.56$, $p = 0.001$). On the other hand, neither Caesarean-delivered gerbil litters (Spearman's *rho* = 0.30, $t(8) = .88$, $p =$ n.s.) nor Caesarean-delivered mouse litters (Spearman's *rho* = −0.12, $t(17) = 0.48$, $p =$ n.s.) exhibited comparable significant correlations between litter size and litter sex ratio. Thus, it was only in litters of vaginally delivered gerbils and hamsters, each examined some hours after parturition, that significant correlations between litter sizes and litter sex ratios were observed.

Regression lines fitted to the sex ratios of individual litters of different sizes in hamsters, mice, and gerbils provide a picture complementary to the correlation coefficients presented earlier. For both vaginally delivered hamsters and vaginally delivered gerbils, the slopes of regression lines fitted to the sex ratios of litters (for hamsters: a = 1.23, b = 0.38 and for gerbils: a = 0.64, b = 0.38) were substantially less than 0.50 and the regression lines passed well above the origin. For both

Table 3
Average Proportion of Males Per Litter by Litter Size and Species

			Gerbils (518)	
L	Hamsters (854)⁺	Mice (1074)	Prepartum (253)	Postpartum (265)
1	1.00(1)	.00(2)*	.33(3)*	.75(4)
2	1.00(2)	.50(2)*	.25(2)*	.70(15)
3	.70(10)	.50(4)	.59(9)	.51(23)
4	.68(14)	.54(6)	.60(17)	.58(19)
5	.57(20)	.58(11)	.47(34)*	.49(36)*
6	.61(38)	.54(24)	.50(51)	.50(52)*
7	.57(71)	.52(30)	.50(73)	.53(44)
8	.54(61)	.55(40)	.48(37)*	.46(42)*
9	.53(103)	.51(68)*	.49(20)*	.42(26)*
10	.47(109)*	.51(112)*	.51(7)	.32(4)*
11	.49(155)*	.51(171)*		
12	.48(107)*	.52(198)		
13	.49(88)*	.54(164)		
14	.47(34)*	.54(134)		
15	.48(21)*	.52(63)		
16	.45(13)*	.53(33)		
17	.41(6)*	.49(8)*		
18	.37(3)*	.39(3)*		
19		–		
20		.40(1)		
Mean	.500 (*8704*)	.525 (*12,450*)	.497 (*1635*)	.490 (*1589*)

L = litter size.
(n) = the number of litters of size L in the sample.
(*n*) = number of pups.
* indicates litter sex ratios lower than the median.
⁺ from Huck, Seger, & Lisk (1990) Table 1.

Caesarian-delivered mice (a = −0.02, b = 0.52) and Caesarian-delivered gerbils (a = 0.15, b = 0.47), the slopes of the regression lines fitted to individual litter sex ratios, as a function of litter size, did not differ appreciably from 0.50, and the regression lines passed very close to the origin.

The finding that the regression lines which, in newborn hamsters, described the correlation between litter size and litter sex ratio both passed well above the origin and had a slope appreciably less than 0.50 was interpreted by Huck et al. (1990) as indicating that, in hamsters, the probability of a conceptus being male varies with its order of conception within its natal litter. In particular, Huck et al. (1990, p. 104) proposed that hamster "litters are assembled according to the following rule: Let the first two ("early") offspring be male with a very high probability, and let each subsequent ("late") offspring be male with a much lower (but approximately constant) probability . . . about 0.38." Such an interpretation of the data rests on the inference that relative litter sex ratios and sizes after birth accurately reflect relative litter sex ratios and sizes before birth.

The differences found in the slopes and intercepts of the regression lines describing the relationships between litter sizes and litter sex ratios in gerbil litters on the days before and after their birth suggest that: (1) there may be substantial perinatal mortality in gerbil litters and (2) this perinatal mortality may be sex biased, with greater perinatal mortality of males in relatively large litters and greater perinatal mortality of females in relatively small litters. The observation that, on the last day of normal gestation, Caesarian-delivered litters contained an average of 6.5 ± .1 live pups, while on the day after birth, vaginally delivered litters contained an average of only 6.0 ± .1 pups indicates that something was killing an average of 0.5 gerbil pups per litter during the perinatal period. The correlation between litter sizes and sex ratios in neonatal gerbil litters appears to result from litter size-correlated, sex-biased perinatal mortality, rather than from litter size-correlated, sex-biased conception.

Our data suggest both that gerbil litters may have been assembled in accord with the relatively simple rule "let each offspring be male with a probability equal to 0.50" and that gerbil litters were disassembled during or after birth in a nonrandom fashion. The same may be true of hamster litters.

Recently parturate gerbils (authors' unpublished observations), like recently parturate hamsters (Day & Galef, 1977), cannibalize some of their pups. Gerbil dams that gave birth to small litters may have cannibalized female offspring more frequently than they cannibalized male offspring. Conversely, gerbil dams that gave birth to larger litters may have cannibalized more male than female young. If so, then both the difference in correlations between litter sex ratios and litter sizes, and the difference in litter sizes observed in Caesarean-delivered and vaginally delivered litters would be explained without postulating deviations from chance in the prenatal sex ratios of gerbil litters.

It should be noted that because we did not randomly assign dams to Caesarian deliver or vaginally deliver their young, the present data only suggest rather than clearly demonstrate perinatal causes of the observed correlation between the litter sex ratios and litter sizes of vaginally delivered gerbil litters.

Expected and Observed Variances in Sex Ratios of Litters

Huck et al. (1990) also analyzed expected and observed variances in the number of males in vaginally delivered hamster litters containing from 3 to 18 pups. As can be seen in Table 4, Huck et al. (1990) found that observed variances were smaller than expected variances in litters of from 3 to 8 hamsters (Sign test, $x = 0, p < 0.00003$). Further, Huck et al. found that observed variances were, on average, only about 70 percent as large as expected variances calculated on the hypothesis that sex determination for each member of a hamster litter was independent. Huck et al. (1990) interpreted such consistently smaller observed than expected variances in the proportion of males/litter as evidence of nonindependence of the probability that each offspring in a litter would be male.

No such departures from independence in sex determination were observed in Caesarean-delivered mouse litters or in either Caesarean- or vaginally delivered gerbil litters. As seen in Table 4: (a) In Caesarean-delivered mice, observed variance in the proportions of males/litter was smaller than expected variance in only 5 of 15 litter sizes and observed variances were, on average, 106.8 percent of expected variances. (b) In Caesarean-delivered gerbil litters, observed variances in proportion of males/litter were smaller than expected variances in 6 of 10 litter sizes and the mean observed variance was 99.3 percent of the mean expected variance. (c) In vaginally delivered gerbil litters, observed variances in proportion

Table 4

Expected and Observed Variances in the Number of Males Per Litter, by Litter Size, and by Species

					Gerbils			
	Hamsters^{+}		Mice		Prepartum		Postpartum	
L	exp	obs(n)	exp	obs(n)	exp	obs(n)	exp	obs(n)
1					.66	.33(3)*	.18	.25(4)
2					.38	.50(2)	.42	.40(15)*
3	.63	.55(10)*			.72	.69(9)*	.72	1.53(23)
4	.87	.37(14)*	.75	1.67(4)	.96	.76(17)*	.98	1.43(19)
5	1.23	1.08(20)*	.99	.57(6)*	1.32	1.24(34)*	1.25	.71(36)*
6	1.43	1.17(38)*	1.22	1.09(11)*	1.60	1.50(51)*	1.50	1.93(52)
7	1.72	1.04(71)*	1.49	1.56(24)	1.72	1.75(73)	1.74	1.35(44)*
8	1.99	1.30(61)*	1.74	1.55(30)*	1.73	2.00(37)	1.99	2.69(42)
9	2.24	1.44(103)*	1.98	2.60(40)*	3.31	2.25(20)*	2.19	2.27(26)
10	2.49	2.13(109)*	2.25	2.45(68)	2.50	3.81(7)	2.19	1.58(4)*
11	2.75	1.88(153)*	2.50	2.87(112)				
12	2.99	1.82(107)*	2.75	3.27(171)				
13	3.25	1.96(88)*	3.00	3.12(198)				
14	3.48	3.17(34)*	3.23	3.88(164)				
15	3.74	2.16(21)*	3.47	3.99(134)				
16	3.96	2.82(13)*	3.74	5.13(63)				
17	4.12	3.61(6)*	3.99	3.44(33)*				
18	4.20	0.34(3)*	4.25	3.64(8)*				
Mean	2.57	1.68	2.48	2.65	1.49	1.48	1.32	1.41

L = litter size.
(n) = the number of litters of size L in the sample.
exp = the expected binomial variance of the number of males in litters of size L. If m is the probability of being male, then exp = $Lm(1-m)$.
* Indicates cases in which the observed variance is smaller than the expected variance.
$^{+}$ From Huck, Seger, & Lisk (1990) Table 3.

of males/litter were smaller than expected variances in only 4 of 10 litter sizes and observed variances were, on average, 106.8 percent of expected variances. Clearly, rules governing the sex composition of litters of hamsters differ from those governing sex composition of litters of mice and gerbils.

General Discussion

The results of the preceding analyses indicate, first, that deviations from random distributions of male and female fetuses both within, and across litters are species specific. Gerbil fetuses are sexually segregated between uterine horns, mouse fetuses are not. Mouse litters are male biased, gerbil, and hamster litters are not, etc.

The data also suggest that postpartum litter sex ratios may not accurately reflect prepartum litter sex ratios. In gerbils, there was a significant correlation between postpartum litter sizes and postpartum litter sex ratios, but not between prepartum litter sizes and prepartum litter sex ratios. Sex-biased cannibalism occurring shortly after parturition may have been responsible for the observed correlation between postpartum litter size and postpartum sex ratio in both gerbils and hamsters.

Such sex bias in litter cannabalism is not totally unexpected on theoretical grounds (Trivers & Willard, 1973). The relative reproductive success of rodents giving birth to relatively small litters might be enhanced if they invested more heavily in sons than did those females giving birth to relatively large litters. If variance in reproductive success of daughters is small relative to variance in reproductive success of sons, and if sons benefit more from a given amount of maternal investment than do daughters, then dams with small litters might increase the reproductive success of their few sons by cannibalizing daughters and investing the resources they would have invested in daughters in sons. To the contrary, females giving birth to large litters with relatively many daughters might increase their reproductive success by cannibalizing sons in whom they could invest relatively little and rearing daughters, not so dependent as sons on maternal investment for their own reproductive success. Hence, one might predict sex-correlated cannibalism in dams, once the size of their respective litters was fixed at parturition.

As discussed in the introduction, litter sex ratios and distributions of male and female fetuses between uterine horns are factors that affect the probability that a male or female fetus will mature adjacent to 0, 1, or 2 fetuses of the opposite sex. Hamsters, gerbils, and mice differ in the ways in which both their litter sex ratios and their distribution of fetuses across uterine horns depart from chance. Consequently, there will be differences in the distributions of phenotypic characteristics affected by intrauterine location in populations of the three litter-bearing, rodent species examined here. Both species specificity in nonrandom distribution of male and female pups and differences in the relationships between litter size and pre- and postpartum litter sex ratios will make it hard to construct generalizations across litter-bearing rodent species that relate litter composition after birth to features of intrauterine life that affect adult characteristics.

Notes

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