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Influence of social factors on sex ratio at birth, maternal investment and young survival in a prosimian primate

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Summary. In order to determine whether social factors influence sex ratio at birth in lesser mouse lemurs, experiments were conducted during 5 successive breeding periods on 51 females. At the beginning of the breeding season, females were either isolated (I) or grouped (G) in heterosexual groups with an increasing number of females (2, 3 or 4). To ensure mating, I females were introduced in a group only during the oestrous period. After mating, both I and G females were isolated during pregnancy and lactation. Reproductive capacities of females in terms of oestrus occurrences ($n=324$), impregnations ($n=210$), pregnancies ($n=136$) or abortions ($n=38$) or litter sizes (1–3 young) were affected neither by age and parity of females nor by group housing prior to conception. G females produced significantly more sons than daughters (67% males for 189 newborn) while females living alone except during the mating period demonstrated a significant inverse tendency (39.6% males for 96 newborn). Distribution of sexes in litters was statistically different from random and varied according to the shift of sex ratio at birth. In G females, the shift in the sex ratio towards males was consistent across the different groups, independent of the number of females living together, suggesting that the presence of only 1 female is sufficient to induce a bias in the sex ratio. No correlation was found between infant survival at weaning and age, parity or group housing of the mother. The maternal investment allocated to male or female newborn was similar provided the litter contained at least 1 male. In litters without males, growth and survival of female infants were significantly less. These results on sex ratio bias in captive female mouse lemurs agree with directions of bias predicted by the local resource competition model for facultative sex ratio adjustment (Clark 1978). Nevertheless, the pattern observed in mouse lemurs appears to be independent of the nutritional state of the female and of differential maternal investment.

Introduction

The lesser mouse lemur, a small polygynous prosimian primate, exhibits a seasonal pattern of reproductive activity which is modulated by social factors in both sexes. In males, physiological and behavioural features of sexual function are highly correlated to dominance-subordination relationships (Perret 1985). In females, life in social groups induces changes in reproductive capacities (Perret 1982, 1986), and as for other prosimians such as *Galago* (Clark 1978) or *Cheirogaleus* (Foerg 1982), a male-biased sex ratio has been observed in offspring of grouped females (Perret 1982).

In several species of mammals, including primates, significantly biased sex ratios of offspring have been interpreted as an adaptive response to environmental factors. Theoretical models of facultative sex ratio adjustment have been proposed in accordance with the general theory of sex allocation (Trivers and Willard 1973; Clark 1978; Maynard-Smith 1980; Clutton-Brock and Iason 1986; Johnson 1988).

The Trivers–Willard hypothesis assumes that females in good condition preferentially produce infants of the sex whose variance in fitness is greater, depending on physical or social characteristics acquired through better maternal investment. In polygynous species, maternal investment is usually recognized as having a greater effect on the fitness of sons than daughters. Females in good condition would thus produce more sons in which they show increased investment, whereas females in poor condition would produce more daughters. Maternal conditions may be affected by different environmental factors such as nutritional state, physical traits related to age and social factors through dominance status or population density. Evidence has been presented in support of the Trivers–Willard hypothesis for each of these parameters and in different mammalian species (Austad and Sunquist 1986; Clutton-Brock et al. 1986; Gosling 1986a; Labov et al. 1986; Huck et al. 1988; Wright and Crawford 1988).

An alternative model, the local resource competition model (LRC), proposed by Clark (1978) and improved by Johnson (1988), predicts that competition between individuals of one sex for access to locally limited resources favours a biased sex ratio towards the oppositve sex. In mammals, females generally are the philopatric sex. Daughters may thus compete with their mothers for local resources, and the sharing of local resources between mother and daughter can be regarded as a form of long-term maternal investment. In this situation, females would minimize competition by biasing the sex ratio of their progeny towards males (Michener 1980;

Verme 1983, 1989; MacShea and Madison 1986; Caley and Nudds 1987). The LRC model leads to a situation inverse to that of the Trivers–Willard model in that females of below average condition would preferentially produce sons to maximize fitness.

Among primates, several examples of sex ratio biases have been reported, but the general issue of the direction or the determinism of the sex ratio bias is often equivocal or controversial since data support either the Trivers–Willard hypothesis (Meikle et al. 1984; Paul and Thommen 1984; MacFarland Symington 1987) or the LRC model (Simpson and Simpson 1982; Silk 1983; Altman 1988; Johnson 1988). These divergent results are difficult to interpret due to the varying social structures found among primates and to the difficulty in assessing which environmental factors affect maternal conditions.

The social structure of the lesser mouse lemur is presently considered as primitive, and a general understanding of their spatial organization is available from field studies (Martin 1973; Lebec 1984; Pages-Feuillade 1988). During the breeding season, females live alone or with affiliative females on small home ranges while males compete to overlap one or more female home ranges. Animals are found solitary when active at night, and food competition is assumed to modulate the degree of overlapping between individual home ranges, thus regulating the distribution and density of wild populations (Perret, in prep.). This pattern of social structure renders the LRC model appropriate. The purpose of this study was thus to determine whether the sex ratio of offspring, survival and growth of the young are modified in lesser mouse lemur females living under different social conditions.

Methods

The 51 female mouse lemurs (*Microcebus murinus*, Cheirogaleinae, Primates) used in this study were laboratory born at Brunoy, from stock originating from the dry forest of the south-western coast of Madagascar. General conditions of captivity have been previously described and were constant with respect to temperature, humidity and ad libitum food availability (Perret 1980).

The reproductive activity of this prosimian primate is photoperiod-dependent and may be artificially induced by long daylengths (Petter-Rousseaux 1975). Animals were therefore exposed to an artificial photoperiodic schedule consisting of 3 months of a short photoperiod (8:16 LD) followed by 5 months of a long photoperiod (14:10 LD). During the active period females may enter oestrus 2 times. In this species, the vagina remains closed except during oestrus, parturition or abortion. Females were examined daily during the peri-oestrous period. Ovulation and copulations were detected by smears during vaginal opening (4–7 days).

All females were studied over 5 successive sexually active periods (including the first sexual activity of young females) and successfully reared at least 1 litter. The age of females varied from 135 days (minimal age recorded at the time of first oestrus) to about 4 years. This age is not considered old for mouse lemurs since in captivity females live for an average of 6–8 years. In this paper, age 1 will refer to the first photoperiodic active period (age of females from 3 to 10 months), age 2 to the second active period (ages from 11 to 18 months) and so forth.

During the resting period (seasonal anoestrus) mouse lemurs are gregarious (Martin 1973), and accordingly females were grouped 2–4 in large cages (1 × 2 × 2 m) or left alone with their young after birth. At the beginning of each active period, females were either randomly isolated (I) or grouped (G) in heterosexual groups of 2 ♂/2 ♀ (G4), 3 ♂/3 ♀ (G6) and 4 ♂/4 ♀ (G8). Several pairs of 1 ♂/♀ were constituted, but this social context led to low reproductive success since females often outranked the male and did not accept mating. In heterosexual groups, the presence of at least 2 males was required to ensure mating success due to the attainment of a dominant status by one of the males (Perret 1985). Among grouped females no clear rank order was observed due to the lack or the variability of aggressive interactions between them.

In all social situations, females entered oestrus 1 month after photoperiodic stimulation. To ensure impregnation, isolated females were placed in a heterosexual group (G4 or G6) when they entered the pro-oestrous period just before perforation of the vulva. On average, these females mated 2 days after introduction into the group. In primates, introduction of an individual into an unfamiliar group is often considered a stressful situation. However, in the mouse lemur, behavioural observations and indirect evidence such as the normal course of oestrus indicated that the isolated female was not affected by stress when introduced into a group for a few days. Moreover, during the oestrous period, social behaviour mainly consisted in male/female interactions, and males behaved similarly with both resident and introduced females.

All females, I and G, were isolated if mated. Females whose vaginal smears did not contain spermatozoa remained in the preceding social environment until the occurrence of the second oestrus of the active period, usually 6 weeks later. The same procedure was then applied for impregnation and isolation of females which were mated.

For all females mated, a positive diagnosis of pregnancy was determined by abdominal palpation about 1 month after mating. This period is half-way through pregnancy since gestation in the lesser mouse lemur lasts about 2 months (Perret 1982a). At birth, litter size and the sex of each offspring (visually distinct from birth) were recorded. Abortion, neonatal and postnatal deaths were also verified. Systematic postnatal measures of the growth of young were performed in 24 sets of twins, infants being weighed every 2 days during the first 10 days, then at 20, 30 and 60 days after birth. All other infants were regularly observed, but body weights were only measured at 30 and 60 days of life. The young were weaned 7 weeks after birth, and when 3 months old, they exhibited body size and dental characteristics typical of adults. Only young who survived the first 60 days of life were considered as successfully reared. The interbirth interval, which is often used to estimate the level of maternal investment, is not useful in mouse lemurs due to the photoperiodic determination of the sexual cycle. In all situations (littering or not, male or female infants), females entered sexual rest when short daylengths were applied and came into oestrus synchronously about 1 month after photoperiodic stimulation.

Statistical analysis. To assure that no bias existed in the interpretation of social influences on reproductive parameters, the distribution of females according to age or parity was verified to be statistically homogeneous within the different social groups used ($\chi^2 = 16$, $df = 12$, NS). To assert statistical differences in population distribution or to test interactions between several factors, we used the χ^2 test and the G test on a 3-way table, respectively. To determine whether the observed sex ratio differed from an equilibrated 50% sex ratio, we employed the paired *t*-test (d = "standardized normal deviate"). Means are indicated with SEM, and differences were tested using one-way analysis of variance. Lastly, linear regression was used to establish possible correlations between parameters.

Results

Fecundity

The fecundity of female mouse lemurs can be evaluated according to several parameters: occurrence of oestrus, impregnation, number of successful pregnancies and litter size. Over the 5 active periods studied, 324 oestruses were recorded and checked by vaginal smears. Oestrus distribution was statistically homogeneous, referring to both age or social context ($\chi^2 = 16$, $df = 12$, NS), indicating that all females entered oestrus at least once during each active period. If no gestation and lactation followed the first oestrus, a second oestrus was observed in 87% of these females.

As a general rule in our captive colony, two-thirds of the females were impregnated. This proportion was independent of group housing ($\chi^2 = 4.89$, $df = 3$, NS) but was significantly increased ($\chi^2 = 4.88$, $df = 1$, $P < 0.04$) for females entering the first oestrus of their life.

Mating did not regularly result in pregnancy and birth. Indeed, from the 210 cases of females impregnated during oestrus, only 136 (64.8%) pregnancies resulted in births. Most successful pregnancies occurred in females impregnated during the first oestrus of the active period (112/136). Normally, few females had the possibility of mating for the second oestrus (including post-partum or post-abortion oestruses) since all females mated during the first oestrus remained isolated until the predicted date of parturition. The mean duration of gestation was 61 ± 0.2 days ($n = 136$) dating from the day when spermatozoa were found in vaginal smears.

Spontaneous abortions with a large vaginal opening and visible foetal remains were observed in 18.1% of the pregnant females at 47.6 ± 1.2 days ($n = 38$) after copulation. However, this incidence of abortion is presumed to be lower than the control value since expulsion or resorption of the embryo may occur prior to the initial diagnosis of pregnancy. This was probably the case for 36 cases of females impregnated during oestrus for which no signs of pregnancy or abortion subsequently appeared. Group housing prior to conception on the age of the females did not significantly modify the result of impregnation: pregnancy, birth or detected abortion ($G = 4.8$, $df = 7$, NS). Likewise, even if females had a propensity for gaining weight with ageing, the body weight of females measured during oestrus was not related to the result of impregnation. Abortive or successfully pregnant females did not differ in body weight when in oestrus: 90 ± 4 g, $n = 38$ and 95.2 ± 2 g, $n = 136$, respectively.

Of the 136 parturitions recorded, 74 (54.8%) consisted of sets of twins, 49 (36%) were sets of triplets, 25 (18%) were singleton births, and there was only one quadruplet birth. Litter size was not significantly affected by social environment or age of mothers ($G = 4.3$, $df = 7$, NS). We noticed a significant increase of the proportion of twins (70%, $P < 0.01$) in primiparous females provided they were in I condition.

Sex ratio at birth

The overall sex ratio (% males) of 285 newborn from the total of 136 litters produced differed significantly from the 50% equality ratio expectation (165 ♂♂/120 ♀♀, sex ratio 57.9%, $d = 2.72$, $P < 0.01$). Sex ratio at birth, parity of the mother and social context prior to conception were found to be dependent ($G = 35.2$, $df = 4$, $P < 0.001$), with no significant interaction between these factors ($G = 0.256$, $df = 1$, NS). Partition analysis demonstrated the significant relationship between sex ratio at birth and group housing of the mother prior to conception ($G = 19.9$, $df = 1$, $P < 0.001$).

When females were maintained in heterosexual groups from the beginning of the sexually active period, they produced significantly more sons than daughters (Fig. 1, 127 ♂♂/62 ♀♀, sex ratio 67.1%; different from 50%, $d = 4.18$, $P < 0.001$), and this shift in the sex ratio was consistent across the different heterosexual groups studied, independent of the number of females (2, 3 or 4) living together. Since grouped females outnumbered isolated ones, the overall sex ratio of newborn was consequently male biased. However, females living alone except during the mating period demonstrated a significant inverse tendency: they produced more daughters (Fig. 1, 38 ♂♂/58 ♀♀, sex ratio 39.6%; different from 50%, $d = 2.04$, $P < 0.05$). This difference in sex ratio of offspring between I and G females is maintained across females of different ages and was not dependent on par-

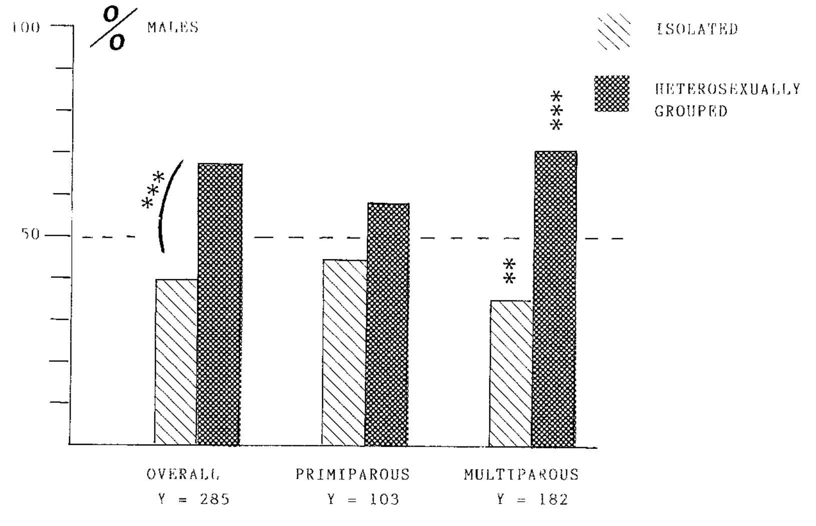

Fig. 1. Sex ratio (% ♂♂) of offspring from 136 litters of lesser mouse lemurs in relation to the social context in which mothers lived prior to conception: isolated (I) (*hatched bars*) or heterosexually grouped (G) (*black bars*). The sex ratio of offspring differed significantly between I and G females (*** $P < 0.001$). The bias of sex ratio towards ♀ in I mothers and towards ♂ in G mothers was not significant in primiparous females but was highly different from a 50% sex ratio in multiparous ones (** $P < 0.02$). Total number of offspring (*Y*) is indicated

ity (G = 2.9, *df* = 1, NS). Nevertheless, when considering only primiparous females, either I or G, the sex ratio of their offspring, though showing the same tendency as multiparous females, did not differ significantly from a 50% sex ratio (Fig. 1).

In several females who gave birth 3–5 times over the five periods studied, there was no tendency for a given female or her lineage to produce preferentially offspring of only one sex. In fact, since each female was subjected to various housing modes and gave birth either to more sons or more daughters according to the respective social context, the sex ratio of all infants produced by one female appeared well balanced at the end of the study.

The sex ratio bias observed in progeny of I and G females was achieved through modifications of the litter composition. We analysed the proportion of litters in which infants of one sex predominated compared with well-balanced litters (the quadruplet birth, 2 ♂♂/2 ♀♀ was not taken into account). The distribution of litter types (Fig. 2) was found to be dependent on both parity and group housing of the mother (G = 50.6, *df* = 7, $P < 0.001$) with a significant interaction between these two factors (G = 6.3, *df* = 2, $P < 0.05$).

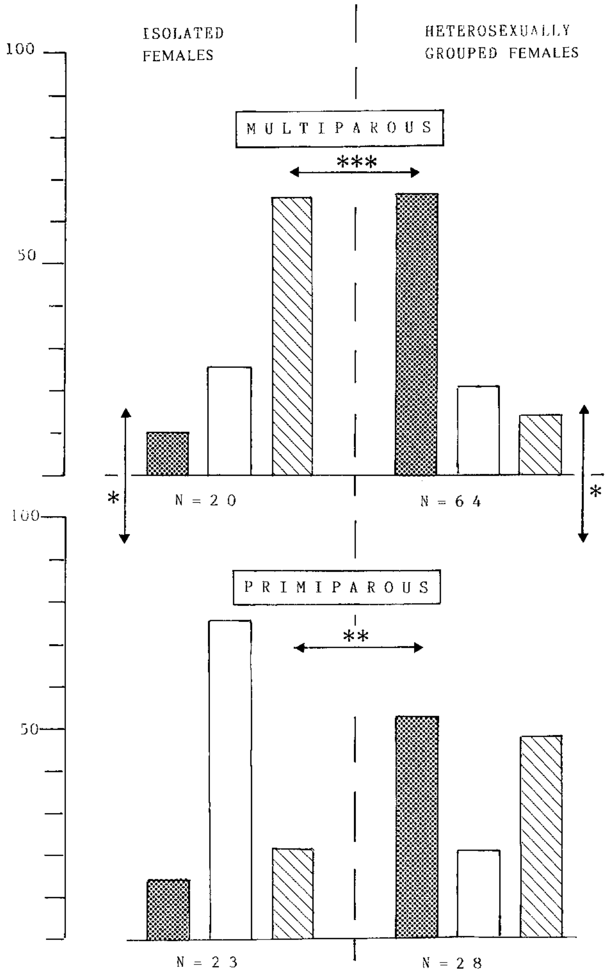

Fig. 2. Relationships between litter composition, parity of the mother and social environment in which mothers lived prior to conception. The proportion of well-balanced litters (*open bars*) and litters in which one sex predominated, either males (*black bar*) or females (*hatched bar*), were compared. Significant differences (* $P<0.05$, ** $P<0.01$, *** $P<0.001$) appeared within the different categories of females. The number of litters is indicated, and in all situations, except for grouped primiparous females, the distribution of males in litters was statistically ($P<0.01$) different from the expected distribution given the probability of a male birth

In multiparous females, the distribution of males in litters was opposite between I and G females (Fig. 2) and was statistically different from the expected distribution given the probability of male birth ($\chi^2 = 8.0$, *df* = 2, $P<0.01$). Litter types were related neither to the size of the litter nor to the age of the female, and among grouped females, the distribution of males in litters was independent of the number of animals living in the group.

The test of independence between parity and litter types was significant (G = 8.32, *df* = 2, $P<0.05$), re-emphasizing that primiparous females did not bias the sex ratio of their offspring as strongly as multiparous females did. For example, no excess of female-dominated litters was observed in primiparous isolated females. They produced mainly well-balanced sets of twins (Fig. 2). However, the distribution of litter types in primiparous females was also significantly different from the expected binomial distribution ($\chi^2 = 13.5$, *df* = 2, $P<0.001$).

Survival of the young

The overall survival of the 285 infants born was 67.4% when considering all young up to the age of 60 days. From this time on (weaning period), infants have an almost 100% chance of surviving to adulthood. Though the survival of the young appeared slightly better in I compared with G females as well as in multiparous compared with primiparous females, none of these differences was statistically significant (Table 1). Similarly, no correlation was found between infant survival and age, lineage or parity of the mother.

In all cases (age, parity, social context) the survival of male infants was higher than that of female infants. We observed that female survival depended upon the composition of the litter in which the young grew up rather than upon the mother's characteristics or upon litter size. In fact, whereas survival of male newborn barely varied around 70%, independently of the litter's

Table 1. Survival of male and female infants at 60 days after birth (percentage young alive/young born) according to parity and social environment of the mother prior to conception. None of the observed differences was statistically significant

	Social context		Parity	
	Isolated	Grouped	Primiparous	Multiparous
♂	78.9	69.3	69.8	72.3
♀	62.1	61.3	58.0	64.3
Total	68.7 (66/96)	66.0 (126/189)	64.1 (66/103)	69.2 (126/182)

sex ratio, female infant survival was highly correlated with the sex ratio of the litter ($r=0.9947$, $df=2$, $P<0.01$), being minimal (36.6%) in litters including only females and maximal (86.6%) in litters with a 2:1 (♂♂:♀) ratio (Table 2).

Most deaths of newborns occurred shortly after birth, i.e. within 5 days post-partum (71 of 93 infants deaths) independent of the social context from which the mother originated or of litter size. Infant mortality mainly resulted from inadequate maternal behavior related to failure of milk production. A significant difference in mortality distribution appeared between the sexes of infants ($\chi^2=4.04$, $df=1$, $P<0.05$) and was again related to litter composition (Fig. 3). In heterosexual litters, infant mortality was similar for both sexes, whereas in litters in which only one sex was present, mortality of male and female neonates differed significantly ($\chi^2=5.8$, $df=1$, $P<0.02$; Fig. 3) since 36.1% additional female newborn died 10–15 days after birth. When only one male was present in the litter, survival of the female newborn was identical to that of the male.

One month after birth, no significant difference in body weight of the young was found between sexes. All

Table 2. Survival of male and female infants at 60 days after birth (percentage young alive/young born) according to sex ratio of the litter from 0% (no males) to 100% (no females). Survival of female infants was highly correlated to the sex ratio of the litter ($r=0.9947$, $P<0.01$), whereas survival of male infants remained constant

Sex ratio of the litter (% ♂♂)	Female survival	Male survival
0%	36.1 (13/36)	–
33%	64.3 (18/28)	71.4 (10/14)
50%	71.8 (28/39)	66.6 (26/39)
66%	86.6 (13/15)	76.6 (23/30)
100%	–	71.2 (57/80)

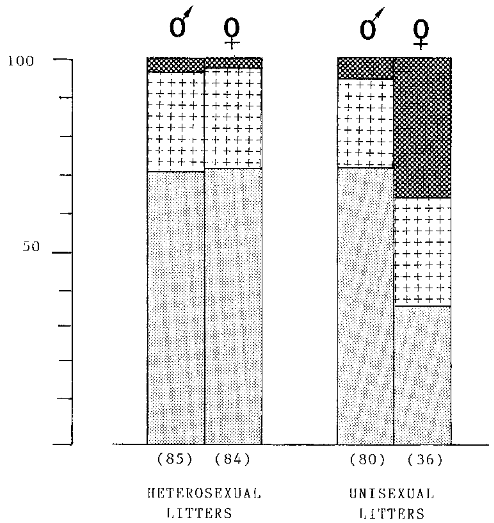

Fig. 3. Proportions of young surviving to 60 days of age (*grey area*), infants dead within 5 days after birth (*crossed area*) and young dead between 10–15 days of life (*hatched area*), according to the composition of litters and sex of the neonates. In unisexual litters, survival of females was significantly lowered ($P<0.001$) owing to their higher mortality at 10–15 days after birth. The number of offspring is indicated in *parentheses*

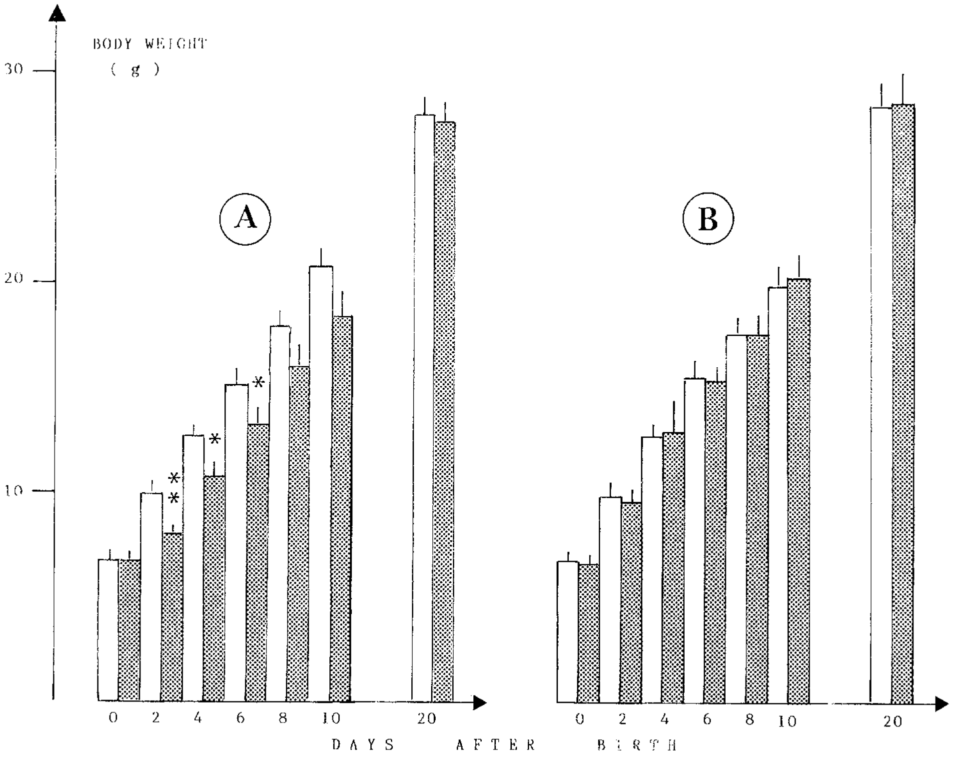

Fig. 4A, B. Changes in body weight of neonates during the first 20 days of life after birth. Male (*open bars*) and female (*black bars*) neonates were reared either as unisexual twins (**A**) or mixed twins (**B**). Means are indicated ± SEM ($n=12$). Significant differences at ** $P<0.01$ and * $P<0.05$

young weighed about 30 g (mean ♂: 30.7 ± 0.5 g, $n = 118$; mean ♀: 31.4 ± 0.8 g, $n = 74$), a value which was not correlated with mothers' or litters' characteristics (size or composition). Likewise, mean body weights were similar at 60 days of age in both sexes (♂: 46.5 ± 0.9, $n = 118$; and ♀: 47.7 ± 1.5 g, $n = 74$).

In terms of survival, the mother's interest or investment towards male or female progeny appeared to differ in the first 2 weeks post-partum. To estimate maternal investment better, the body weight of young from 24 sets of twins were recorded: 12 consisted of 1 ♂/1 ♀, 6 were 2 ♂♂ and 6 were 2 ♀♀. All mothers were experienced.

At birth, mean body weight of neonates was similar in male and female neonates (♂ 6.8 ± 0.3 g, $n = 24$; ♀ = 6.6 ± 0.2 g, $n = 24$). The growth of male infants was independent of litter composition (Fig. 4), reaching about 20 g 10 days after birth, corresponding to a growth rate of 1.34 ± 0.06 g/day. On the contrary, the growth of female neonates changed according to whether or not a male newborn was present in the litter (Fig. 4). When there was no male in the litter, the body weight of infant females increased more slowly than that of males of the same age, and the difference was significant up to 8–10 days post-partum (from $P < 0.05$ to $P < 0.01$; Fig. 4). For these females growing in unisexual litters, the growth rate was 1.15 ± 0.07 g/day. Thereafter, the difference lessened and completely disappeared at 20 days after birth. On the other hand, when a male was present in the litter, the growth rate of female neonates was entirely comparable with that of male infants, suggesting that in lesser mouse lemurs, the maternal investment allocated to male or female newborn was similar when the litter contained at least one male.

Discussion

Sex ratio bias and stress

In captive mouse lemurs, the direction of the sex ratio bias of offspring in females, either towards daughters in isolated females or towards sons in grouped females, could at first be considered as a response to changes in density, since captive females lived in groups with from 1 to 8 individuals. Increasing or inadequate social interactions within a group or a population have been interpreted as factors capable of modifying the sex ratio of progeny in females (Schaik and Noordwijk 1983; Gosling 1986a; Pratt and Lisk 1989). Several studies report a male bias of offspring in females in poor condition resulting from stress of increased density or subordinate social status (Silk 1983; Verme 1983; Armitage 1987; Jones 1988). Interpreted in terms of the Trivers–Willard hypothesis, stressed females would produce male-biased offspring to maximize theit fitness, given that litter size is smaller than average (McGinley 1984; Krackow and Hoeck 1989). This interpretation has been discussed (Gosling 1986a; Caley and Nudds 1987; Verme 1989) but is inadequate to explain the variation of sex ratio observed in captive mouse lemurs for several reasons.

First, according to this hypothesis, one would expect to find a small litter size associated with a male sex ratio bias in grouped mouse lemur females. However, no differences in litter sizes were observed in relation to group housing, and no correlation was found between sex ratio and size of litters.

Second, if social stress was a factor acting to bias the sex ratio, the male bias would be related either to the number of animals per group, to the dominance relationships among grouped females or to stress associated with the introduction into an unfamiliar group for isolated females. However, the sex ratio bias is opposite between I and G females and agrees with previous observations of sex ratio bias between paired and grouped females (Perret 1982). No clear dominance relationships appeared to be present among grouped females and in all heterosexual groups used, the bias of sex ratio towards males is similar and independent of the number of females per group. Moreover, the male bias is also found in paired females which are able to communicate through olfactory, visual and auditory signals (Perret 1982).

Finally, following the assumption that the sex ratio bias is dependent on the mother's condition, we might suppose that grouped females were in poor condition compared with isolated females. Previous studies on female mouse lemurs have shown that life in groups led to a decrease in reproductive capacity such as an increasing frequency of abortions and premature births, high neonatal deaths and low survival of infants (Perret 1982). These observations were made on females exposed to long-term social stress for periods of at least 6 months. In the present experiment, females were grouped only for short periods, i.e. less than 1.5 months, thus avoiding the effects of long-term social stress. Under these housing conditions, no decrease in reproductive capacity was observed in grouped females and the number of oestruses, pregnancies or abortions was similar in all females. Likewise, survival of both male and female young was not correlated with either housing prior to conception or parity. All females, multiparous or not, isolated or not, showed identical capacities of investing in progeny.

The LRC model

While the male sex ratio bias of offspring in grouped females cannot be explained by stress, our data suggest that in captive mouse lemurs it is nevertheless linked to the presence of females living in the same area, as has been reported in other mammals (MacShea and Madison 1986; Armitage 1987; Jones 1988; Verme 1989). Since female mouse lemurs are philopatric, female or male offspring will be preferentially produced, depending on the density of resident females, thus reducing competition between females as predicted in the LRC model (Clark 1978).

In mouse lemurs, this pattern of sex ratio variation towards the sex that has the higher chance of reproductive success appears to be independent of the nutritional state of the female and furthermore independent of the cost of producing individuals of that sex as suggested by Armitage (1987). Indeed, a difference in sex ratio at birth was not associated with changes in infant survival. Moreover, maternal investment allocated to male or female newborn was similar provided the litter contained at least one male, implying that the presence of a male newborn promotes maternal behaviour, a pattern also observed in neonatal rats and attributed to olfactory interactions between mother and young (Moore 1979, 1985). This effect appears to be restricted to a short time after birth and could be related to the neonatal secretion of androgens by males (Corbier et al. 1978; Moore and Samonte 1986).

Determinism of sex ratio bias

Different mechanisms have been invoked for the post-conceptual regulation of sex ratio, such as higher mortality of one sex before or after birth (Clutton-Brock et al. 1985; Gosling 1986b; Pratt and Lisk 1989) or selective destruction of one sex in the litter (MacClure 1981). None of these occur in mouse lemurs, which show stable litter sizes, suggesting that the sex ratio bias in the female mouse lemur occurs pre-conceptually.

Concerning a model based on pre-conceptual influences, several results indicate that the physiological state of the female can bias the sex ratio at the time of copulation. For example, Y-bearing spermatozoa migrate faster (James 1980, 1985a) and copulation before ovulation is recognized to favour the production of males (James 1980). In mouse lemurs, females were almost always mated at the time of vaginal opening, i.e. before ovulation which normally occurs on the third day of vaginal opening (Perret 1982). Although this mating behaviour could favour a male bias, males behaved identically with both introduced or resident females.

Differences between isolated and grouped females leading to a pre-conceptual bias probably occur before oestrus in relation to hormonal differences. Indeed, in humans, high levels of gonadotropins at the time of conception have been associated with a significant excess of female births (James 1985a, b). Levels of gonadotropins are correlated with hormonal secretions during the follicular phase (Goodman and Hodgen 1983), and in mouse lemurs, hormonal levels throughout the ovarian cycles can be strongly modified by the presence of other females (Perret 1986). When females are reared together, several modifications are observed: lengthening of the oestrous cycle, abnormal luteal phase, increasing number of atretic follicles (Perret 1980) and high cortisol levels (Perret 1986). All these changes indicate an inappropriate secretion of gonadotropin hormones at the time of ovulation. They are absent in females living without intrasexual competition but occur when 2 females communicate through olfactory and auditory signals (Perret 1986). It is thus plausible that life in close proximity for females at the beginning of the breeding season or at least during the 15-day follicular phase would influence and perhaps disrupt the normal development of ovarian follicles if female density is high. This would result in lower gonadotropin secretion at the time of ovulation and accordingly, would favour the production of males in grouped females. A similar explanation could also account for the male-biased sex ratio of offspring in subordinated or stressed females, for which sexual hormone profiles are known to be impaired (Abbott 1987).

The reduced response of young females to the presence of another female suggests that hormonal secretions during the first oestrous cycle are less sensitive to social factors than during the following oestruses. This mechanism is probably an important feature of sex ratio regulation in wild populations. Whereas male offspring disperse before the breeding season, daughters stay with their mothers at least until the first seasonal oestrus. The young females disperse at a later time (when pregnant) because females become highly intolerant at that time.

The pattern of sex ratio variation in mouse lemurs according to social context raises the question as to whether in other mammals, sex ratio biases and differential maternal investment could also be determined by physiological mechanisms involving maternal hormones at conception or neonate hormones at birth. Due to the importance of olfactory cues in the regulation of sexual hormones in mouse lemurs (Schilling and Perret 1987), it would be of interest to determine the way in which chemical signals may be involved in the control of these physiological mechanisms.

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