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PARENTAL INVESTMENT IN THE COMMON MARMOSET (*CALLITHRIX JACCHUS*): DEMOGRAPHY AND BEHAVIOR

A Thesis

Presented for the

Master of Arts

Degree

The University of Tennessee, Knoxville

Karen Lisa Bales

August 1995

DEDICATION

To my family

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ABSTRACT

This research attempted to determine if the common marmoset (Callithrix jacchus, family Callitrichidae) is biasing its sex ratio and parental investment according to patterns predicted by Trivers and Willard (1973) and other current investment theory. Because the common marmoset has a polyandrous mating structure and high female reproductive variance, females in good condition were predicted to invest more in female infants and females in poor condition were predicted to invest more in male infants. Both demographic and behavioral data sets were examined.

Demographic data sets from Oak Ridge Associated Universities Marmoset Research Center and the University of Tennessee Walters Life Science Colony were analyzed. Sex ratios were compared to frequencies of the cumulative binomial distribution. Interbirth intervals of females in poor and good condition were compared by the Kruskal-Wallis test. Data from Walters Life Science were compared to that of ORAU by means of Fisher's method for combining probabilities. Demographic data showed a bias towards females in all births and a bias towards females born to mothers in good condition.

Behavioral data was collected at the Walters Life Science colony. Infant carrying was analyzed by condition of the mother, while nursing and food provisioning behavior was also analyzed by condition of the infant. Some relationships were observed qualitatively, although multivariate analysis was impossible due to the small sample size.

It was concluded that a bias exists in the predicted direction in the birth sex ratio of the common marmoset. Some behavioral biases also exist according to the condition of the mother and the infants involved.

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CHAPTER I

INTRODUCTION

Sex ratio and parental investment theory originated in the work of population geneticist R.A. Fisher. In his 1930 book The Genetical Theory of Natural Selection, he suggested that, assuming that the costs of producing sons and daughters is equal, selection in the population as a whole would favor an equal sex ratio at conception through pressure to produce the less common of the two sexes. Deviations in the sex ratio would result from 1) differences in the cost of raising sons and daughters and 2) differences in the expected reproductive success of sons and daughters. Any deviations should exactly cancel out in the population and should be highly unstable (O'Brien and Robinson 1987). Other population geneticists (Shaw and Mohler 1953) have continued to work with sex ratio adjustments and modelled "Environmentally Stable Strategies" which predict the reproductive success of a mutant female producing a sex ratio different from the norm.

Trivers and Willard (1973) modified previous hypotheses to account for extremely skewed sex ratios in some populations. Trivers had previously defined parental investment as "any investment by the parent in an individual

offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (1972, p.139). A mother with extra resources to invest would be expected to produce more of the sex with the greatest variance in reproductive success, assuming that her extra resources would give this offspring a competitive edge. In species with higher male variance in reproduction, more parental investment leading to a bigger, healthier male would be predicted to greatly increase his reproductive success at the expense of other males. The lower variance in female reproductive success would mean less return for extra resources invested, along with less risk and the assurance of at least some return. Parents in these species in good condition would thus be expected to bias their reproduction towards males. This hypothesis has been studied in many species, including primates.

Work in non-human primates has resulted in a competing hypothesis, called local resource competition (Table 1). Clark (1978) first suggested this idea as a result of her work with galagos, a female-philopatric species. She hypothesized that, in a species where one sex is philopatric and grown offspring will be competing with their mother for resources, females might be expected to bias their reproduction towards the dispersing sex. Silk (1983) incorporated the idea of "rank" interpreted as "condition";

Table 1. Summary of Trivers-Willard and Local Resource Competition Hypotheses.

Model	Trivers-Willard (1973)	Local Resource Competition; Clark (1978), Silk (1983)
Basic Assumptions	Mothers act to maximize genetic fitness	Mothers act to maximize genetic fitness
	Mother's condition has a greater effect on one sex than the other	Mother's condition has a greater effect on one sex than the other;mo. competes with grown offspring of philopatric sex
	Mothers in good condition, through superior nutrition, etc.,confer an extra advantage on the sex with the higher variance in reproductive success (RS)	Mothers in good condition, through maternal rank, confer an extra advantage on the philopatric sex
	Mothers in good condition will invest more in the sex with the higher reproductive var.; mothers in poor condition will invest more in the sex with the lower repro. variance	Mothers in good condition will inv. more in the philopatric sex; mothers in poor condition will invest more in the dispersing sex
Species usually Studied	Many insects, fish, reptiles, and non-primate mammals; mostly polygynous or promisc. mammals	Mostly Old World monkeys (cercopithecines) female-philopatric with male dispersal
Prediction for Most Mothers in Good Condition	Invest in males	Invest in females
Prediction for Most Mothers in Poor Condition	Invest in females	Invest in males

high-ranking mothers were assumed to have better access to resources, receive less aggression, etc., and therefore be in superior condition, and vice versa for low-ranking mothers. She suggested that in social systems such as many macaques, where one sex is philopatric and inherits the mother's rank, high-ranking mothers would bias reproduction towards the philopatric sex (in macaques, females) and low-ranking mothers towards the dispersing sex (males). However, as van Schaik and Hrdy (1991) pointed out, the Trivers-Willard and local resource competition hypotheses are not mutually exclusive and could apply simultaneously to the same population. They suggested that, especially in cercopithecine societies, when resource competition is relaxed, Trivers-Willard effects will predominate; when competition is intense, the selective pressures predicted by the local resource competition hypothesis will become more important.

Williams (1979) and later McGinley (1984) modelled a continuum of expected maternal investment dependent on the condition of the mother. They suggested that sex ratio variation is not a simple dichotomy, and, for instance, in a species which normally twins, mothers in the worst condition would have one child of the cheaper sex, slightly better condition one child of the more expensive sex, then two cheap children, etc.. Gosling (1986b) discussed the models

created by Williams and McGinley and emphasized their limitations. For instance, mothers may not produce the maximum possible offspring value at any one time in order to maximize lifetime reproduction. Precise measures of parental investment ability are needed and should be measured by a mother's nutrient or fat reserves. This parental investment ability may be manifested at various stages of development, including preconception (Guerrero 1974, Harlap 1979, James 1989), prenatal (Erwin and Anderson 1975), and post-natal (Cronk 1989, Trillmich 1986).

Most studies of non-human primate parental investment and sex ratio adjustment have been conducted on Old World monkeys such as macaques and baboons, and have often been testing the local resource competition hypothesis (Silk 1983, 1988; Silk et al. 1981; Koyama et al. 1992; Paul and Thommen 1984; Simpson and Simpson 1982; Small and Smith 1985). These animals are all characterized by female philopatry. The only New World primates in which these effects have been studied are capuchins (O'Brien and Robinson 1987) and spider monkeys (McFarland Symington 1987). Some studies found support for the local resource competition hypothesis and some did not (see Chapter II for a summary). No callitrichids have been studied for biases in sex ratio according to condition of the mother. It is important to test hypotheses in situations where the predictions are opposite to those normally made. The common

marmoset offers an opportunity to make some of these predictions; in particular, females in good condition will be expected to invest more in females, and females in poor condition will be expected to invest more in males.

Common marmosets are small New World monkeys (Callithrix jacchus, family Callitrichidae) which exhibit what has been thought to be a polyandrous, communally breeding social structure (Sussman and Garber 1987). Females are typically 1.02 times the size of males (Ralls 1976). This compares to a male/female size ratio of 0.91 in Macaca mulatta, 0.51 in Macaca radiata, and 0.53 in Papio cynocephalus, species in which sex ratio studies have been performed (Fedigan 1992). Normally the dominant female in a callitrichid social grouping suppresses reproduction in all other females in the group and tends to mate promiscuously (Sussman and Garber 1987, p.81). Females usually give birth to twins, which are cared for by most group members including the adult males and other siblings. Aggression between adult females is high and is attributed to an attempt to gain exclusive access to males as reproductive partners and caregivers. However, this view of common marmoset social structure is currently under revision as differences between callitrichid species become more clear. Some researchers lean towards a view of Callithrix groups as highly stable families (Ferrari and Digby 1993). In addition, observations of wild social groups of Callithrix

jacchus have established that, at least in some cases, there may be more than one breeding female per group. However, reproduction by subordinate females still appears to be severely curtailed (Digby 1994).

Thus in both sexual dimorphism and in social structure common marmosets are almost diametrically opposed to the polygynous mammals on which studies of Trivers-Willard effects have usually been tested and very different from the Old World monkeys on which most primate studies have been conducted. This species offers a good opportunity to test predictions opposite to those which have previously been made.

I. Statement of Purpose

The purpose of this thesis is to determine if the common marmoset (Callithrix jacchus) is biasing its sex ratio and post-natal parental investment according to patterns predicted by Trivers and Willard (1973). To achieve this purpose, both demographic and behavioral data have been examined. Demographic data from the Oak Ridge Associated Universities Marmoset Research Facility, which contains full pedigrees and breeding histories for many females, were used. Behavioral data was collected from the Walters Life Science Marmoset Colony on the University of Tennessee, Knoxville, campus, administered by Dr. Suzette

Tardif under NIH grant number (R01-RR02022). The following hypotheses and predictions were tested:

H1. Mothers in good condition (large absolute size, large fat reserves, increasing or maintaining weight) are expected to invest more in female infants than in male infants.

Prediction 1: Mothers in good condition will bear more female infants than male infants.

Prediction 2: Mothers in good condition will carry female infants more than male infants.

Prediction 3: Mothers in good condition will nurse female infants more than male infants.

Prediction 4: Mothers in good condition will provision female infants more than male infants.

H2. Mothers in poor condition (small absolute size, small fat reserves, decreasing weight) are expected to invest more in male infants than in female infants.

Prediction 1: Mothers in poor condition will bear more male infants than female infants.

Prediction 2: Mothers in poor condition will carry male infants more than female infants.

Prediction 3: Mothers in poor condition will nurse male infants more than female infants.

Prediction 4: Mothers in poor condition will provision male infants more than female infants.

H3. All mothers are expected to invest more in a higher birth weight or behaviorally more advanced (defined by markers such as time first seen off, time first eating solid food, etc.) infant than in a lower birth weight or less advanced infant; however, mothers in better condition are predicted to invest more in both infants than those in worse condition.

Prediction 1: Mothers in good condition are predicted to invest more (bear more infants, carry, nurse, and provision infants) on an absolute scale than mothers in worse condition.

Prediction 2: All mothers are predicted carry, nurse, and provision a higher birth weight or more behaviorally advanced infant more than a lower birth weight or less behaviorally advanced infant.

H4. Demographic records of mothers in poor condition (as defined by clinical treatment during pregnancy) are expected to show a higher sex ratio (more males) when compared to mothers in good condition (who received no treatment).

H5. Mothers in poor condition are expected to show reproductive depression, in the form of a longer interbirth interval, after raising two females than two males or one of each sex. Mothers in good condition are expected to suffer no reproductive depression.

CHAPTER II

LITERATURE REVIEW

In this chapter I will review some empirical studies of sex ratio variation both in non-primate mammals and in primates. I will then briefly discuss proposed mechanisms for sex ratio adjustment, as well as their applicability (or lack thereof) to the common marmoset. Finally, I will discuss the social system and infant development of the common marmoset and its relevance to parental investment theory.

I. Sex Ratio Studies

A. Mammalian Sex Ratio

Sex ratio variation has now been studied in many mammalian groups, including mice, voles, hump-backed whales, and several species of deer (for a summary see Clutton-Brock and Iason 1986). Clutton-Brock and Iason state that sex ratio studies are handicapped by "a lack of consistent variation, the dubious statistical basis of many suggested trends, the paucity of evidence for genetic variation in sex

ratios, and the absence of any known mechanism by which sex ratios at birth can be manipulated" (p.339). For instance, non-significant results have been used to support or dispute hypotheses. In a reanalysis of 108 sex ratio trends in the literature, Clutton-Brock and Iason found only 44% (some of which were in primates) to show significant variation according to their criteria. However, there are several fairly well-established trends as well as some seminal mammalian sex ratio studies in laboratory and wild groups. In most mammals other than primates, the researchers have tested the Trivers-Willard hypothesis rather than the local resource competition hypothesis.

Many studies on laboratory animals have looked at nutritional and stress effects on sex ratio (Clutton-Brock and Iason 1986; Bronson 1989). McClure (1981) showed that restricting a pregnant female's food intake led to a low sex ratio (more female offspring) in the wood rat (Neotoma floridana), while Austad and Sunquist (1986) found an increase in numbers of male offspring of provisioned females in the opossum (Didelphus virginianus). Rivers and Crawford (1974), and Labov et al. (1986) both found significant effects of restricted diet on sex ratio, favoring daughters, in nutritionally stressed laboratory mice and hamsters (Table 2). These results are all consistent with the Trivers-Willard hypothesis.

Table 2. Some Studies of Species Sex Ratio Based on Maternal Condition in which Significant Variation was Found. The studies in the top half supported the Trivers-Willard hypothesis and those in the bottom half supported the local resource competition hypothesis. "S.R." refers to sex ratio and the term underneath is the condition of the animal.

Species	Social Structure	S.R. Poor	S.R. Control	S.R. Good	P-Value	Citation
Neotoma floridana wood rat	polygynous	0.40 (at 20 d)	1.0		.05	McClure 1981
Didelphis marsupialis opossum	polygynous		1.0	1.33	.007	Austad & Sunquist 1986
Mus musculus mouse	promisc. mating	0.32	1.02		.05	Rivers & Crawford 1974
Mesocricetus auratus golden hamster	promisc. mating	0.69	0.98		.003	Labov et al.,1986
Cervus elaphus red deer	polygynous	0.88 low rank	1.17 medium rank	1.54 high rank	.05	Clutton-Brock et al.,1984
Papio cynocephalus savanna baboon	daughters inherit maternal rank	2.00		0.29		Altmann et al., 1988
Macaca sylvanus Barbary macaque	daughters inherit maternal rank	0.91	0.96	1.38	.05	Paul & Keuster, 1990
Macaca radiata bonnet macaque	daughters inherit maternal rank	2.20		1.35	.0023	Silk et al.,1981
Ateles paniscus spider monkey	daughters disperse	0.0 no males		1.09	.0001	McFarland Symington 1987

One particularly important field study is that of the ecology of red deer (Cervus elaphus) (Gomendio et al. 1990; Clutton-Brock 1988, 1991). Red deer are polygynous mammals and therefore expected to have high male reproductive variance. Gomendio and Clutton-Brock looked at female survival and reproductive performance according to the sex of the infant to which they had just given birth. They found that the birth of sons depressed the survival of subordinate mothers but did not affect that of dominant mothers, and that subordinate mothers that bore males were less likely to bear a calf the following year. They attributed this phenomenon to the increased cost of investing in a son, which fell disproportionately on subordinate mothers.

Gosling studied selective abortion in the coypu (Myocastor coypus, family Myocastoridae). He dissected wild-caught female coypu, sexing their embryos and recently-dead embryos, as well as determining the size of aborted litters from abortion scars. He found that young mothers in good condition aborted small or predominantly female litters but not larger or predominantly male litters. Gosling determined that females in good condition that aborted their litters usually conceived between 1.13 and 1.65 extra offspring afterwards (1986a).

These results tend to support the operation of Trivers-Willard effects in the species studied, all of which are

either polygynous or promiscuous, in that mothers in poor condition tended to have a lower sex ratio and mothers in good condition tended to have a higher sex ratio. However, it must be emphasized that a great number of sex ratio studies have not yielded significant results. The results of other studies depend on large and perhaps confounding assumptions. For instance, Wiley and Clapham (1993) found a male-biased sex ratio in humpback whale mothers in good condition. However, their results hinged on their definition of good condition in this animal, which is a long interbirth interval. Interbirth interval is more commonly used as a measure of maternal investment or reproductive depression; therefore as a dependent, rather than an independent, variable. Rejection of interbirth interval as a measure of good condition would bring their conclusions into question. Independent variables of studies have included maternal condition, rank, and age, as well as ecological conditions such as seasonality. The dependent variables usually measured are sex ratio and interbirth interval.

B. Non-Human Primate Sex Ratio

As noted above, Clark (1978) introduced the local resource competition hypothesis as a result of her work with galagos (Galago crassicaudatus). Since then, with a few

exceptions, research on primate sex ratio has been performed mostly in Old World monkeys such as macaques and baboons, and has been testing this hypothesis. Variables of interest have included primary and secondary sex ratio, interbirth interval, and reproductive success. Most studies equated rank with the condition of the mother, although most did not have information on the mothers' physical condition. Unfortunately, few if any studies have extended far enough to determine the lifetime reproductive success of individuals.

Silk et al. (1981) and Silk (1983, 1988) examined the local resource competition hypothesis in bonnet macaques (Macaca radiata). They found that differences in reproductive success between females were primarily due to infant survival, and that daughters of low-ranking females were subjected to more harassment than males. They did not find effects of infant sex on interbirth interval or maternal mortality, but did find a high sex ratio among low-ranking females in infants surviving to 1 and 24 months. They interpreted their results as supporting the local resource competition hypothesis, in that that mothers in poor condition (low-ranking) raised more infants of the dispersing sex.

Simpson and Simpson (1982) looked at over 20 years of sex ratio records in a captive colony of rhesus macaques (Macaca mulatta) in which maternal dominance rank was known.

They found that high-ranking mothers were more likely to give birth to daughters, while all other mothers were more likely to give birth to sons. Altmann et al. (1988), studying savannah baboons (Papio cynocephalus) in Amboseli National Park, Kenya, also found a large skew in sex ratio shortly after conception. They extrapolated this sex ratio from the birth sex ratio, claiming that pregnancy could be detected shortly after implantation and few miscarriages occurred afterward. High-ranking mothers produced a ratio of three to four females to one male, while low-ranking mothers produced a ratio of two males to each female. The strong skew indicates support for the local resource competition hypothesis, which would predict investment by low-ranking mothers in males and by high-ranking mothers in females. They also suggest an effect of the mother's rank on offspring survivorship, further skewing the sex ratio. Paul and Keuster (1990), however, found a bias towards daughters in the offspring of low-ranking females, and a bias towards sons in high-ranking females in Barbary macaques (Macaca sylvanus), supporting the Trivers-Willard hypothesis.

The data on cercopithecine sex ratio are not all so clearcut. Wasser and Norton (1993), in a 17-year demographic study of free-ranging baboons (Papio cynocephalus) in Mikimi National Park, Tanzania, found differences in offspring sex ratio according to the season

and other ecological conditions, but not the mother's rank or condition. Rhine (1992, 1994), analyzing 21 years of reproductive data on captive stump-tailed macaques (Macaca arctoides), found no relationship between a mother's dominance rank and offspring sex ratio. Finally, in a 30-year study of provisioned Japanese macaques, Koyama et al. (1992) found no effect of the female's rank-class on annual birth rate, infant mortality, or offspring sex ratio.

There have been very few studies of sex ratio and parental investment in apes or New World monkeys. The only study in apes, Mace (1990) studying captive gorillas (Gorilla), did not look at sex ratio by mother's condition but did find a trend for sex ratio to decrease with the age of the mother. In New World monkeys, capuchins and spider monkeys have been studied. Robinson and O'Brien (1991) found that the sex ratio in a population of free-ranging wedge-capped capuchins (Cebus olivaceus) correlated with group size, and that the population sex ratio was strongly skewed towards daughters. Finally, McFarland Symington (1987) studied sex ratio in wild spider monkeys (Ateles paniscus), a species which is male-philopatric with female dispersal, and therefore the opposite of many cercopithecine societies. She found a strongly female-biased sex ratio for the entire population and the phenomenon of lower-ranking females producing daughters exclusively. This study argues strongly in favor of the local resource competition

hypothesis, not only because of the statistical strength of its findings, but because it was conducted on a wild population and because the social system of spider monkeys allows the testing of hypotheses opposite to those looked at in other studies.

Why have some sex ratio studies of primates found significant variation while others have not? There may be several reasons. First, the populations in question are living in very different ecological conditions. Although some of the populations in which significant variation was found were free-ranging and some were captive, most of the populations in which variation was not found were either captive or provisioned (i.e. Koyama et al. 1992, Rhine 1992, 1994). Theoretically, provisioning or ad lib feeding in a captive situation would tend to reduce differences in maternal condition. Secondly, many measures of parental investment are poorly operationalized; for instance, interbirth interval has been used as an indication or relative maternal investment or reproductive depression (or even maternal condition in the Wiley and Clapham whale study). Rank is very often used as a measure of maternal condition with no physical data to link the two. Third, some variables have yet to be measured: for example, the "cost" of offspring remaining on a home territory has been hypothesized to be higher because of food competition or lower because of offspring helping behavior, but data are

usually not presented to back up these assertions. Reproductive variance is also often left unquantified.

Primate studies are prime offenders in the problems mentioned above. None of the primate studies referenced here in any way connect rank of the mother back to measures of maternal condition such as fat reserves. Many do not discuss the species's reproductive variance, or if they do they merely assume that a polygynous species will have a greater male variance. To be fair, a greater reproductive variance in one sex than the other is not an explicit requirement of the local resource competition hypothesis, which most primate studies are testing. One of the best primate studies as far as meeting the criteria above is Paul and Keuster (1990). Although they do not provide data to link mother's rank to her condition, they perform their study on a semifree-ranging population and do estimate reproductive success.

Studies of non-primate mammals in general do a better job of defining maternal condition, either because weights are taken or differences in maternal condition are induced by food restriction or provisioning. No one study meets all the criteria above, but Austad and Sunquist (1986), Wolff (1988), and Clutton-Brock et al. (1984, 1988) come close.

Another reason for the variation in results may be the marginality of the phenomenon in mammals overall, and a final reason the lack of any known mechanism for sex ratio

adjustment prenatally. The mechanisms which have been proposed, but not proven, are discussed in the next section.

C. Mechanism for Sex Ratio Variation

As stated earlier, it has been hypothesized that mammalian mothers can influence the sex ratio of their future offspring both before and after conception. The support for any one proposed mechanism is not necessarily very strong, and several hypotheses are of limited applicability to the common marmoset. In addition, the sex ratio at conception is very hard to get at in many mammals (especially in field studies) and therefore relatively little data are available on primary sex ratio. I will therefore cover this topic briefly.

1. Pre-conception

There are two main hypotheses for post-copulatory, pre-conception sex ratio adjustment mechanisms in mammals, both characterized by a relationship between sex ratio and coital frequency: hormonal regulation correlated with timing of fertilization, and differential X and Y sperm motility.

Guerrero (1974) and Harlap (1979) originally reported that, in humans, the regression of sex ratio on cycle-day of natural insemination is U-shaped, with more females being conceived near the time of ovulation, and more males early

and late in the fertile period. Gray (1991) reviewed six studies of natural family planning and reaffirmed their conclusions. Supposedly, increased coital frequency during the fertile period would serve to increase the chances of insemination earlier in the period and therefore to raise the sex ratio. James (1989, 1987a-b, 1986) is one of the most prolific advocates of the hormonal regulation of the sex ratio and relationship of sex ratio to time of insemination within the female cycle. He claimed that high levels of testosterone and estrogen at the time of conception are associated with male offspring and high levels of gonadotropin with female offspring. He also asserted that in humans and voles there is "a strong presumption" that the relationship is causal. James cited sex ratio data from other studies of rodents, primates, and ungulates.

Martin (1994) criticized both James' logic and the data which his model was developed to explain (Guerrero and Harlap's results). According to Martin, James' logic is faulty because he ignores the fact that there are two parts of the fertile period, one before ovulation in which fertilization might eventually result but is dependent on sperm survivorship, and one at ovulation and for a day or two afterwards in which immediate conception is possible. In addition, Martin claimed that most of the significance of the chi-square in Guerrero's data comes from

inseminations two days after ovulation, and in Harlap's data from inseminations three to eight days before ovulation. He questioned the equivalence of the two patterns and concluded, from the fact that women in Guerrero's data set were reportedly inseminated up to nine days before ovulation and human sperm are usually only effective for two to three days, that many women in the sample were irregular or early ovulators.

The opposing theory is that increasing coital frequency will increase the sex ratio (Martin 1994). This is portrayed as a competition between sex cells with different strategies. Y-bearing spermatozoa are initially advantaged by their greater motility but lose this advantage as more X-bearing cells reach the uterus. Frequent intercourse will provide more extra mobile Y-sperm and thus raise the sex ratio at conception. Differences in motility of X- and Y-sperm have been demonstrated in tests in which sperm are allowed to swim up a column of fluid, and in tests which have recovered an excess of Y-sperm (X- and Y- produced initially at an equal rate) postcoitally from the cervix and uterus (Roberts 1978). Motility of sperm has also been shown to be correlated to fertility in men (Bruno et al. 1986). However, Roberts (1978) also pointed out the fact that differential motility cannot be used to explain any excesses of female conceptions.

2. Post-conception

Post-conception mechanisms for influencing the sex ratio of offspring have been suggested for both before and after birth. One of these mechanisms, the "harassed daughter" hypothesis, may not be applicable to callitrichid groups. However, since this is the proximate mechanism suggested in many studies of primate sex ratio, I mention it here, and then discuss post-natal mechanisms, which are more applicable to the animals used in this study.

The mechanism which has been suggested for post-conception, pre-birth sex ratio adjustment in cercopithecines, the primates in which the local resource competition hypothesis has primarily been tested, is the "harassed daughter" hypothesis. In female-philopatric primate societies such as macaques, harassment of females pregnant with female fetuses has been observed. Sackett (1981) found that female pigtail macaques pregnant with female infants received significantly more bite wounds than those pregnant with males (N= 2822 conceptions in 1308 females). Erwin and Anderson (1975) had previously suggested that the secretion of androgens by male fetuses may masculinize the behavior of the pregnant female. Nieuwenhuijsen et al. (1988) examined the aggressive behavior of pregnant females to determine if behavioral

differences in the mothers as a result of fetal gender might be responsible for differential aggression, and found no clear effect. It must be emphasized that this proposed mechanism would not be applicable to callitrichid groups, where the breeding female does not receive significant intragroup aggression.

3. Post-natal

There are several kinds of evidence that mammalian parents bias their investment post-natally. These are: sex differences in early growth and offspring body size; differences in the energetic "costs" of raising males and females; and differences in the reproductive costs of producing males and females (Clutton-Brock 1991). Parental energetic effort or "expenditure", such as lactation, is generally used as a close correlate of parental investment (Ortiz et al. 1984). Post-natal differential investment is an important topic for this thesis because of the nature of the behavioral data collected and because of its plausibility as a proximate mechanism for adjustment of sex ratio.

Sex differences in juvenile growth may be misleading because of different growth priorities or activity patterns in the two sexes (Duncan, Harvey and Wells 1984). Differences in juvenile growth between the sexes in the

common marmoset have not been found (Jaquish 1993), however, differential energy expenditure by the parents is possible; it has not been measured. Indeed, differences in juvenile growth in common marmosets are not expected based on their lack of adult sexual dimorphism.

Energetic costs of investing in sons and daughters may differ, especially in highly dimorphic mammals. For instance, in fur seals (Arctocephalus), male infants consume up to 61% more milk by volume than female infants, although when plotted against mass sex differences in milk intake are not significant (Trillmich 1986, Costa and Gentry 1986). Suckling time may also be measured behaviorally, although it can be unreliable because weaker infants may take longer to suckle or be forced to the less productive teats. Mendl and Paul (1989), studying house mice and domestic cats (Felis catus) found a significant inverse relationship between offspring suckling time and growth rate for both species. They suggested that the inverse relationship is due to offspring demand rather than milk transfer rate.

Male and female infants may also produce different reproductive costs for mothers; for instance, decreased survival or fecundity for the mother of an infant of a specific sex, or a longer interbirth interval until the next litter. For instance, in the study of red deer mentioned above, subordinate mothers that gave birth to sons experienced a longer interbirth interval and reduced

survivorship compared to those who bore daughters (Clutton-Brock et al. 1984). Another study which documented reduction in reproductive performance as a correlate of sex ratio was conducted with American bison (Wolff 1988). Wolff found that cows nursed sons longer, and that cows that had sons were more likely to be barren the next year.

A complicating factor in the study of post-natal bias in parental investment is the greater juvenile mortality demonstrated by male mammals (Clutton-Brock 1991). The juvenile period is defined as the period between infancy and puberty (Walters 1987). In primates, the higher juvenile male mortality has been attributed to the lower fat reserves and higher growth rates of males, presumably making them more vulnerable during times of food shortage (van Schaik and de Visser 1991). In humans (at least in modern Western populations) the sex ratio declines significantly even before birth due to higher male fetal deaths (McMillen 1979, Kellokumpu-Lehtinen and Pelliniemi 1984). However, Jaquish (1993) found no sex effect on survivorship of the common marmoset up to six months of age.

D. Other Offspring Characteristics

Offspring characteristics other than sex might be expected to influence parental investment decisions. These might include offspring quality and offspring behavioral

development. Parents of many species discriminate between offspring on the basis of size, although discrimination within litters by mammalian mothers has not been extensively studied (Clutton-Brock 1991). There is some evidence that ewes with twins attempt to equalize milk intake during later stages of lactation by allowing suckling only if both lambs suckle at once (Ewbank 1964). Goat mothers are thought to attempt to compensate for the weaker member of a pair of offspring by extensively licking the more vigorous offspring and thus delaying its initial suckling (Klopfer and Klopfer 1977). A study of a pair of twin rhesus macaques, however, documented the behavioral preference of the mother for the larger twin (Spencer-Booth 1968).

In humans, Mann (1992) conducted behavioral observations of extremely low birth weight twins. Her data indicated that mothers consistently favored the less sick of the two infants, and even when the overall level of investment was high, the smaller/sicker twin received less attention.

Behavioral characteristics of common marmoset infants may affect parental investment behavior and in turn be affected by it. Marmoset infants that steal food more often tend to be smaller than those that receive more food shares (Jaquish 1993).

E. Summary

The literature on parental investment and sex ratio adjustment is varied and far-ranging. For a study of parental investment in the common marmoset, the most informative literature is probably that regarding mammals other than primates and testing the Trivers-Willard hypothesis. Because most callitrichid groups contain only one reproductively active female, the concept of maternal rank is not applicable. In addition, the social structure of the common marmoset has several interesting features which make it ideal for a test of the Trivers-Willard rather than local resource competition hypothesis.

II. The Common Marmoset

A. Social Organization

Several salient features of callitrichid social organization have already been discussed above. However, the following points are worth re-emphasizing. Traditionally, and according to most previously available field studies, callitrichid social groups were characterized as containing only one reproductively active female, who suppressed ovulation in all subordinate females. The

presence of more than one adult male and participation of the subordinate male in infant carrying led to the characterization of callitrichid groups as polyandrous (Sussman and Kinzey 1984; Goldizen 1987; Sussman and Garber 1987). The most relevant factor of social organization for the Trivers-Willard hypothesis, however, is high reproductive variance in at least one of the sexes.

Recent studies have led to some qualification of these ideas. Dietz and Baker (1993), studying golden lion tamarins (Leontopithecus rosalia) in Brazil, found polygyny in 10% of their study groups. In these cases, the two breeding females were usually mother-daughter and the older female was usually dominant. However, the reproductive success of the subordinate female was notably lower. The mean number of offspring surviving to a given date per reproductive female per sample period for dominant females was 0.684 ± 1.108 (N=19), and for subordinate females 0.333 ± 0.617 (N=15). These data give some indication that even in polygynous groups a high level of female reproductive variance exists.

Digby (1994), studying the common marmoset, found two breeding females in all three of her study groups. However, the subordinate female's reproductive success was severely limited and one case of infanticide of a subordinate female's infant was witnessed, with the dominant female as the suspected culprit. The dominant females in her study

achieved 62% offspring survivorship, while only 33% of subordinate females' offspring survived. There were also non-reproductive adult females in these groups. Because successful emigration appears to be fairly unlikely (Digby witnessed no instances of it, and hers is the only extensive field study of the common marmoset) and the costs of dispersal high, it is possible that many females may never reproduce at all. Thus, the main requirement for the Trivers-Willard model, high female reproductive variance, is still upheld by current views of callitrichid social organization.

B. Infant Development

The callitrichids are generally considered to be communally breeding primates. Adult males and older siblings participate in carrying and licking offspring (Goldizen 1987). Infants also receive some amount of solid food provisioning, food shared by parents or older siblings. This may consist of an active set of behaviors including eye contact, food presenting, and a food call (Brown and Mack 1978), or a more passive acceptance by other group members of the infant eating from or taking the other group members' food (Tardif et al. 1993, Simek 1988). Callitrichid infants are generally carried for the first three weeks postnatally, after which they become increasingly independent and are

rarely carried after the age of 8-12 weeks (Yamamato 1993). Parents differ in caregiving behavior according to previous experience gained as helpers and, in primiparous mothers, according to levels of urinary estradiol, thus affecting their tendency to retrieve crying infants and to harass infants (bite the infant, rub it against the side of the cage, etc., in an attempt to get another carrier to retrieve it or to force it to move off on its own) (Pryce 1993). Tamarins tend to show a longer carrying period than marmosets. Weaning occurs during weeks 8-15, and at first all solid food eaten may be provisioned (Yamamato 1993). In practice, interspecific and individual variation in infant care practices is high. There are also differences in caregiving acts between non-reproductive helpers of different sexes (Baker 1993).

In summary, callitrichids display many unique characteristics which make them ideal for a study of parental investment and sex ratio. In this study, I examined demographic records of Callithrix jacchus for sex ratio bias, and conducted post-natal behavioral observations to explore the relationships between maternal condition, infant condition, and infant sex.

CHAPTER III

MEANS AND METHODS

I. Subjects

A. The Oak Ridge Marmoset and Tamarin Research Facility

The Oak Ridge Associated Universities Marmoset Research Center has maintained a colony of marmosets and tamarins since its inception in the early 1960's by Dr. Nazareth Gengozian. The animals are fed the BAM diet (bananas, apple sauce, monkey chow, and vitamin and mineral supplements) in the morning, and a canned diet (Zupreem Marmoset Diet, Hill's Pet Products, Topeka, Kansas) along with dietary supplements, in the afternoon (Clapp and Tardif 1985). Extensive demographic information is available on these animals, including the full reproductive histories of many females.

Some of the animals owned by Charles River Laboratories and housed at the Oak Ridge colony were found to be infected by a pancreatic nematode and considered to be in inferior condition, based on weight gain, clinical histories, etc., to the other animals (Hawkins, personal communication). Therefore two gross categories of poor and good condition

exist upon which sex ratio of offspring may be compared in the demographic analysis.

B. Walters Life Science Colony

All animals used in behavioral research were housed at the Animal Care Facility in the Walters Life Science Building on the University of Tennessee, Knoxville, campus. They were housed in mesh cages (1.83 m. wide, 1.52 m. tall, and 0.91 m. deep) with natural wood perches and removable nestboxes, in rooms kept at 80 $\pm$ 4 degrees Fahrenheit. Cages were separated visually from each other by means of metal partitions and plastic curtains. Animals were kept in natural family groupings and infants remain in their groups through several consecutive litters. These animals are fed a homogeneous, semi-purified diet which should not significantly nutritionally stress any of the animals. Feeding is administered twice a day, at 8:00 am and 3:00 pm, in sufficient quantity to be considered ad lib. The mothers and infants in this behavioral analysis are participants in a reproductive study (NIH grant R01-RR02022 to Dr. Suzette Tardif) which involves conducting ultrasound examinations of females during pregnancy, post-partum laparoscopic exams on the mothers, and of body compositions and milk intake studies involving both the mother and infants.

II. Demographic Analyses

A. Goals

The goals of the demographic analyses were to investigate Hypotheses 4 and 5 regarding the relationship between the condition of the mother, the sex ratio of the offspring, and the interbirth interval, used as a measure of reproductive depression. Demographic information from both colonies was used in these analyses.

B. Oak Ridge Colony

As stated above, clinical information was available to assist in the classification of females as being in poor or good condition. I classified females that were treated in the course of a pregnancy (usually for diarrhea) as being in poor condition. Age-matched females were chosen from the group of females for whom there is no record either of clinical treatment or a fecal result positive for nematodes. Reproductive records of females of both conditions were analyzed using the Kruskal-Wallis test to assess the effects of condition, litter size, and the sex of the offspring on interbirth interval (Sokal and Rohlf 1981). The sex ratio of infants born following the interbirth interval was

analyzed both for the ratio at birth and the ratio surviving one month, using expected frequencies of the cumulative binomial distribution. Tests were first performed against a standard 50:50 chance of giving birth to either a male or female. However, most primates and indeed most mammals have a slightly male-biased sex ratio fetally and at birth (Clutton-Brock 1982). Taking man as typical primate for whom population-wide sex ratios are known, tests were also performed with a 51.5:48.5 probability (Roberts 1978, McMillen 1979, Novitski and Sandler 1956). Computer analyses were done using SAS Statistical Software (SAS Institute, Cary, NC). Further detail on the demographic analyses is included in Chapter IV. In addition, demographic records of sex ratio from the Walters Life Science colony were included for comparison (see below).

C. Walters Life Science

Demographic information available from the Walters Life Science colony was also analyzed for comparison with Oak Ridge. Because of the standardized, high quality living conditions of the Walters Life Science colony, it is unlikely that any of the females in the behavioral sample could be classified as being in poor condition. In fact, they are all in the middle to upper range for body size for this species (Lunn 1983). However, they do differ in their

size and fat reserves and therefore their potential for parental investment. Body weights on every animal in this colony are collected every week by introduction of a digital scale into the cage and recording approximately 10 weights on each animal. This is the same method used by Jaquish (1993), including the same model and brand of scale, and who found repeatability of weights on a given individual for one session to be 0.99. For many females, body composition data are also available. Data collected from these females indicate that the positive correlation between body weight and fat reserves is strong (Tardif, unpublished data).

For an analysis of maternal condition relative to sex ratio at birth, mothers were classified as being in better or worse condition. This classification was made according to body weight during early pregnancy. Research indicates that body weight 50 - 60 days into pregnancy (which lasts approximately 148 days) is a good estimate of non-pregnant weight (Lunn 1983). In addition, research in humans indicates that early pregnancy weight is a strong determinant of many factors associated with outcome of pregnancy, for instance infant birth weight (Neggers et al. 1995). Relative weight gain or loss is also important for many investment measures in these animals (i.e. ovulation number, litter size reduction) and was used for classification for some behavioral analyses (see below) (Tardif and Jaquish 1994). However, many of the pregnancies

in this analysis were the female's first pregnancy in this colony and therefore relative body weights were not available. A range of weights from around 50 - 60 days into pregnancy were averaged for a female's baseline body weight for each pregnancy. Although the range of weights appears to overlap considerably, when the mean weights for this time period are taken, females group relatively confidently into animals between 310 - 325 g and animals over 350 g (Table 3). This method of classification does mean that the potential exists for females to be in both categories, and one animal was (female 018).

III. Behavioral analyses

A. Goals

The goals of the behavioral analyses were to test Hypotheses 1, 2, and 3, regarding the relationship between infant sex, infant condition, and maternal condition. To do so, behavioral observations were carried out from 5/11/94 to 5/28/95 on animals from the Walters Life Science colony.

B. Methods

To assist in distinguishing twins from each other, one of each pair of infants was marked, usually the day

Table 3. Average baseline weights for females (early pregnancy).

Female Number	Average Baseline Weight (g), mean ± s.d.
001	358.6 ± 11.8
002	410.9 ± 4.0
003a	319.1 ± 3.6
003b	322.0 ± 9.5
018a	323.7 ± 13.6
018b	357.2 ± 8.2
018c	325.4 ± 11.4
024	373.6 ± 3.5
028	403.1 ± 20.0
030	327.3 ± 3.1

after birth, using "Thirty Minute Bleach", a commercial bleaching product (Figure 1). The other infant was removed at the same time and subjected to approximately the same procedures, i.e. its fur was wetted, etc.. It was hoped that in this way each infant was exposed to the same potential stressors. No behavioral differentiation by the parents between marked and unmarked infants was noted. Focal observations using continuous sampling were carried out twice a day, once in the morning and once in the afternoon, for the first two weeks of life (see next section for definitions of behaviors and types of data collected). After the first two weeks, observations were carried out three times a week to four months of age. Due to time constraints, observations on two litters of infants were concluded after two months and one litter after three weeks. In addition, observations on one litter ended early (three weeks) due to the accidental death of the infant during a caretaking procedure. Observations were conducted for 30 minutes, with each infant being focal for 15 minutes, although full information was generally collected on both. The observer was concealed behind a one-way blind during all observations. The observer remained blind to both the sex and weight of the infants during the period of observations. Observations were carried out by myself, Dr. Suzette Tardif, and Lisa Drummer, an ethology graduate student. They were either recorded on audio tape and transcribed later, or

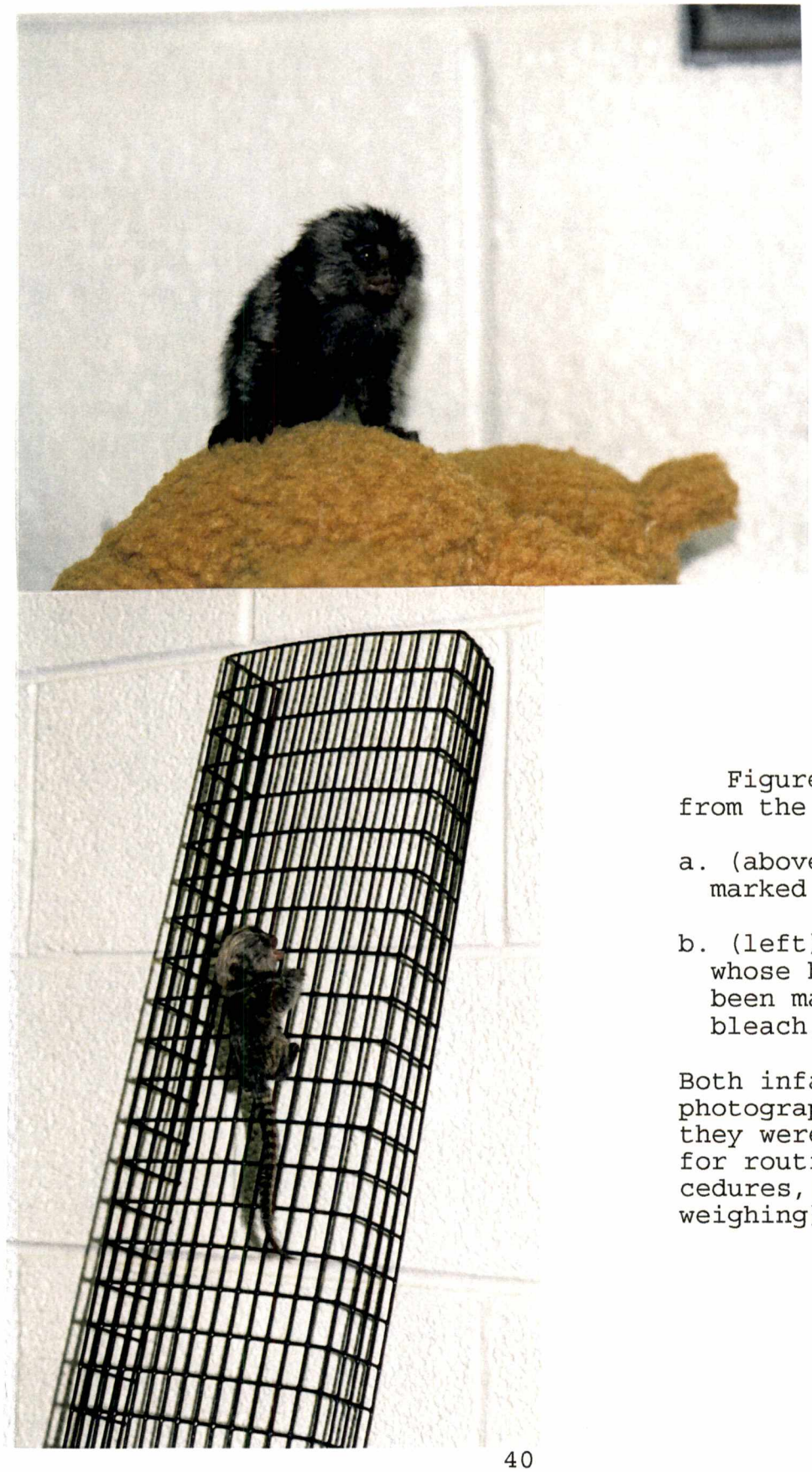


Figure 1. Infants from the WLS colony.

a. (above) An unmarked infant.

b. (left) An infant whose head has been marked with bleach.

Both infants were photographed when they were removed for routine procedures, (e.g. weighing).

taken on a IBM laptop computer running Noldus behavioral software (Observer 3.0).

C. Behavioral definitions

Specific behaviors recorded, and the type of information collected, include:

Carry- the infant is clinging to another animal using at least two limbs, and the other animal appears to be bearing the infant's weight. The identity of the carrier was also noted. Duration.

Nurse- the infant's head is axial (under the armpit) on the mother. Duration.

Off- the infant is clinging independently to the cage or on a perch. Duration.

Cry- the infant is making distress calls. Duration.

Investigate- a group member is grooming or examining the infant. The identity of the group member was noted. Frequency.

Harass- a group member is biting at an infant, pulling parts of its body, rubbing it on the side of the cage, etc., usually while carrying it. The identity of the group member was noted. Frequency.

Eat- the infant is ingesting the experimental diet. Durations of eating were measured according to processing time, i.e. how long the infant's mouth was moving. Any ingestions of other substances, such as bark, were noted but not included in analysis. Any liquid intake by the infant was also noted. Duration.

Food Beg- the infant approaches another group member which has food, usually making a "crying" noise. The identity of the group member was noted. Frequency.

Food Share- the infant is allowed to eat off or take another group member's food with no resistance (i.e. chittering, moving away) within ten seconds before or after. Notes were made according to whether or not the infant was allowed to take the entire piece of food, and as to the identity of the group member. Duration.

Food Steal- the infant eats off or takes another group member's food despite resistance. Notes were again made according to whether or not the infant took the entire piece

of food, and as to the identity of the group member.

Duration.

D. Classification of Mothers for Behavioral Analysis

The condition of mothers was reclassified for each time period of behavioral analysis. The first period of behavioral analysis was the first three weeks postpartum, which is approximately the amount of time that the infant is nourished solely by milk (Yamamato 1993). For this period mothers were classified by their immediate postpartum body weight. The second period of behavioral analysis was three weeks to two months postpartum, a weaning period, for which mothers were classified by their weight gain or loss relative to their baseline early pregnancy body weight. The third period of behavioral analysis, from two to four months postpartum, is a period of minimal to no investment in the form of lactation on the part of the mother, but possibly of investment in the form of food provisioning. For this period mothers were also classified in terms of relative weight gain or loss.

IV. Summary

Both demographic and behavioral information was collected to address questions of infant sex ratio and

maternal condition. I used behavioral data from the Walters Life Science marmoset colony to address Hypotheses 1, 2, and 3, which predict the amount of investment, in the form of carrying, nursing, and food provisioning, that females will allocate to infants of different sexes and conditions. These results were analyzed through use of descriptive statistics. I used demographic data from the Oak Ridge and Walters Life Science colonies to address Hypotheses 4 and 5, testing the results with frequencies of the cumulative binomial distribution, the Kruskal-Wallis test, and Fisher's method for combining probabilities.

CHAPTER IV

DEMOGRAPHIC ANALYSIS

I. Oak Ridge Colony

A. Whole colony sex ratio

The sex ratio of all Callithrix jacchus births in the Oak Ridge colony is female-biased (sex ratio= .88, p=.06, cumulative binomial probability). Hypothesis 4 predicts that the healthy mothers would have a lower (more female-biased) sex ratio than the mothers in poor condition (sex ratio is defined as number of males/ number of females). In fact, removing successively broader groups of females which can be classified as in poor condition increases the significance of the bias (Table 4). Removal of just the specific litters whose mothers were treated during the pregnancy increases the bias to .876 (p=.06). Removal of all litters of those mothers increases the bias to .85 (p=.04), and removal of all litters whose mothers have a record of a positive test for nematodes increases the bias to .84 (p=.03). These biases are all in the direction predicted.

Table 4. Demographic Analysis of Sex Ratio of the Common Marmoset, Oak Ridge and Walters Life Science Colonies. N = total number of infants. S.R. = Males/Females. The first p-value is for analysis at 50:50 and the second at 51.5:48.5.

Sample	N	S.R.	% males	P-Value
All jacchus births in the Oak Ridge colony	628	0.88	46.8%	.06, .01
O.R. births minus litters where mother treated during preg.	606	0.876	46.7%	.06, .01
Oak Ridge births minus all litters of treated mothers	541	0.85	46.0%	.04, .01
Oak Ridge births minus all litters of mothers who tested pos. for parasites	502	0.84	45.6%	.03, .005
Mothers treated during pregnancy; all infants born	22	1.00	50.0%	.58, .53
Mothers treated during preg.; infants surviving one month	13	0.62	38.5%	.29, .25
Age-matched mothers who were not treated; all infants born	27	0.59	37.0%	.12, .09 (.08, .06 combined with WLS)
Age-matched mothers not treated; infants surviving one month	19	0.46	31.6%	.08, .07 (.05, .04 combined with WLS)
WLS lighter mothers; all infants born	10	1.00	50.0%	.62, .59
Lighter mothers; infants raised	8	0.60	37.5%	.36, .33
WLS heavier mothers; all infants born	13	0.44	30.8%	.13, .11 (.08, .06 combined w/ORAU)
Heavier mothers; infants raised	6	0.20	16.7%	.11, .10 (.05, .04)

The above probabilities are based on the assumption of a 50:50 chance of each individual infant being either male or female. In fact, it is common in mammals to have a slightly male biased sex ratio fetally and at birth (Clutton-Brock 1982). There is no reason to think that most primates would be any different than a typical mammal in this respect. The sex ratio at birth has been most comprehensively studied in humans (Roberts 1978, McMillen 1979, Novitski and Sandler 1956), and is usually stated at around 1.06 (51.5% male). Taking man as a typical primate with a slight male bias at birth, the sex ratios for the colony were reanalyzed at a 51.5:48.5 probability. The probability for the whole colony sex ratio was p=.01. Probabilities for the other analyses at a 51.5:48.5 probability are also included in Table 4.

B. Analysis of interbirth interval

In the analysis of interbirth interval, I attempted to answer three questions: Does female condition have an effect on her reproduction (length of interbirth interval and survival of infants) ? Does the sex of the offspring a female is raising differentially affect the length of her interbirth interval depending on her health? Is the offspring sex ratio at the end of the pregnancy biased according to the condition of the mother? To answer these

questions, I used interbirth interval as a measure of reproductive depression, as in Clutton-Brock (1984). Sample selection for interbirth interval analysis has previously been described. Because the distribution of intervals was non-normal (Figure 2), the Kruskal-Wallis test, a non-parametric, distribution-free test, was used in lieu of an ANOVA. The sample used was described in Chapter III, and consisted of twelve pregnancies of mothers in poor condition and twelve pregnancies of mothers in good condition.

The illness of the mother clearly lengthens her interbirth interval between offspring (Figure 3). The mean interbirth interval for healthy mothers is 198 days and that of unhealthy mothers is 264 days ($p=.03$, $N=24$). Mothers in poor condition gave birth to 22 infants, 13 of which survived; mothers in good condition gave birth to 27 infants, 19 of which survived. A chi-square analysis revealed no difference in offspring survival between mothers in poor and good health ($p=.70$).

As a possible confounding factor in looking at the effect of sex ratio on reproduction, the litter size raised was also considered. Litter size did not affect the interbirth interval of heavier mothers ($p=.38$, $N=12$). However, mothers in poor condition showed a tendency to have longer interbirth intervals when raising two offspring rather than zero or one ($p=.11$, $N=12$) (Figure 4). The sex ratio of the infants raised did not affect the interbirth

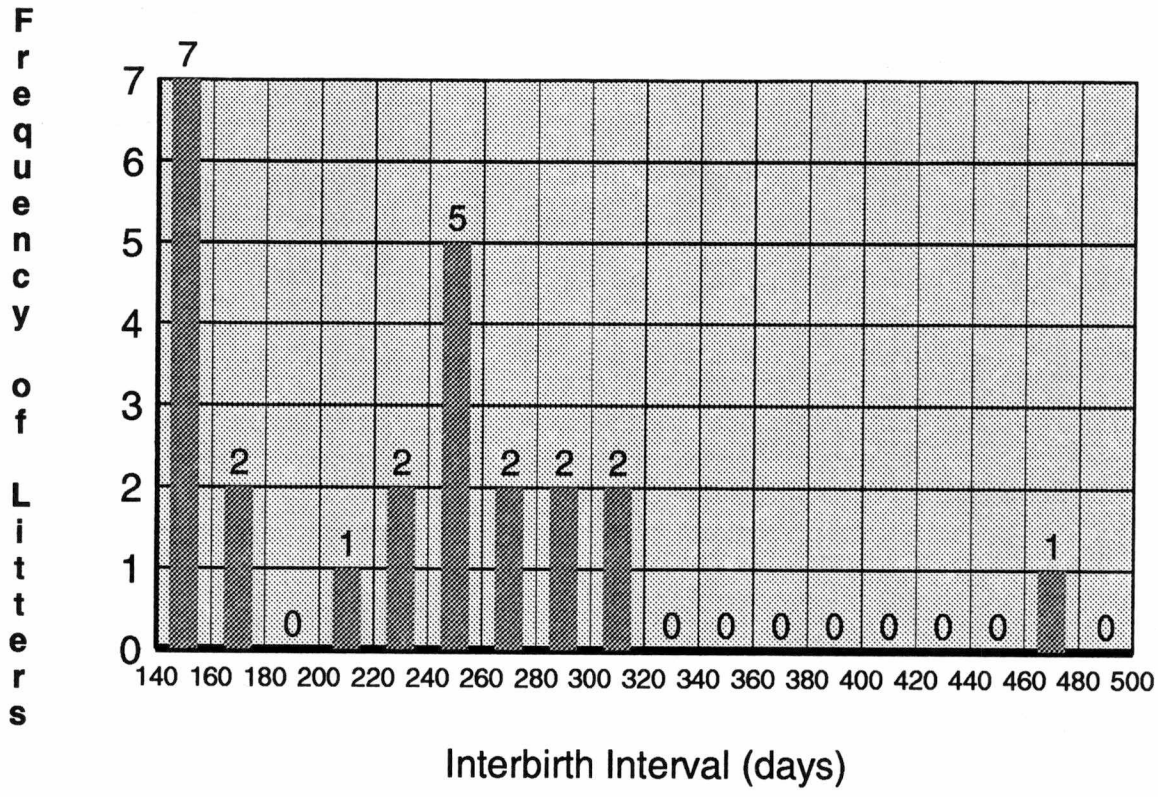


Figure 2. Distribution of Interbirth Intervals, Oak Ridge Marmosets. The distribution is non-normal, with two peaks (N=24).

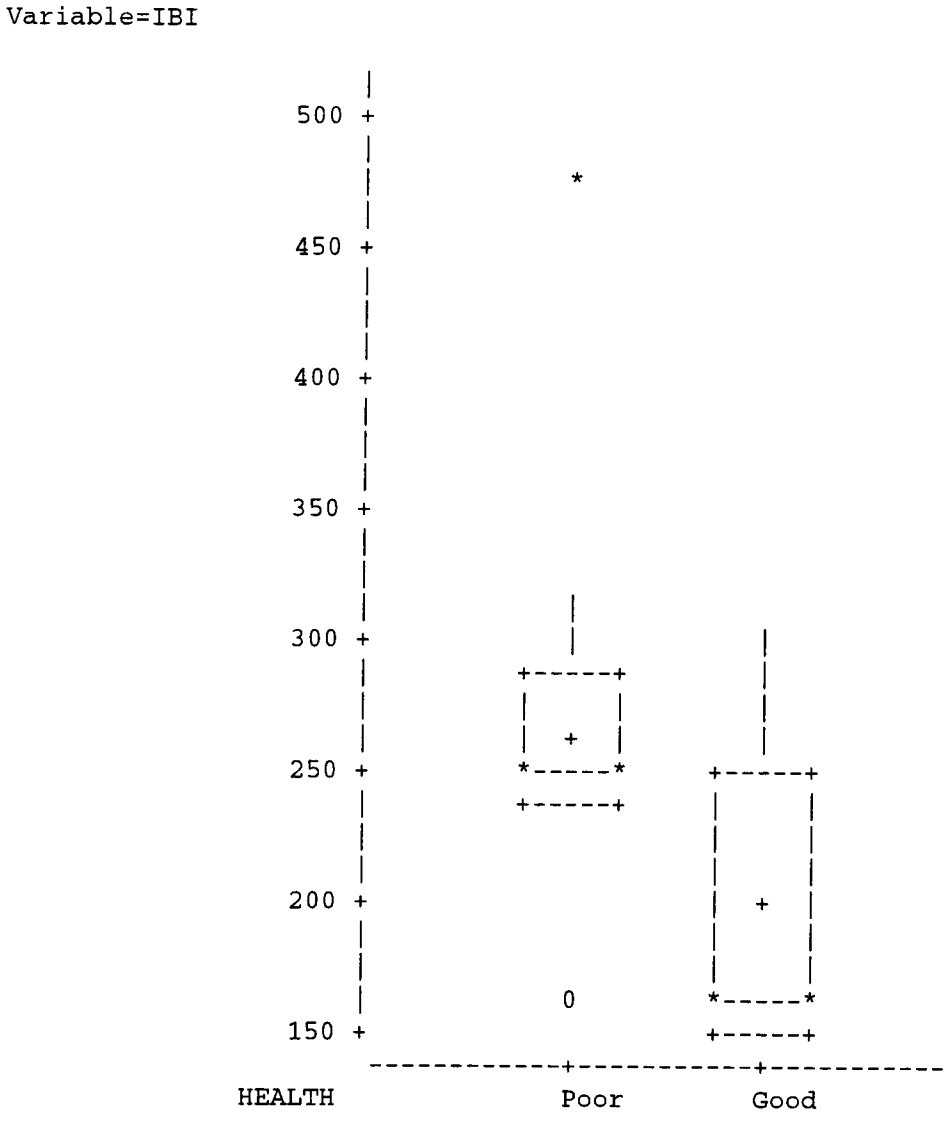


Figure 3. Analysis of Interbirth Interval by the Health of the Mother. Illness clearly lengthens interbirth interval (p=.03, N=24).

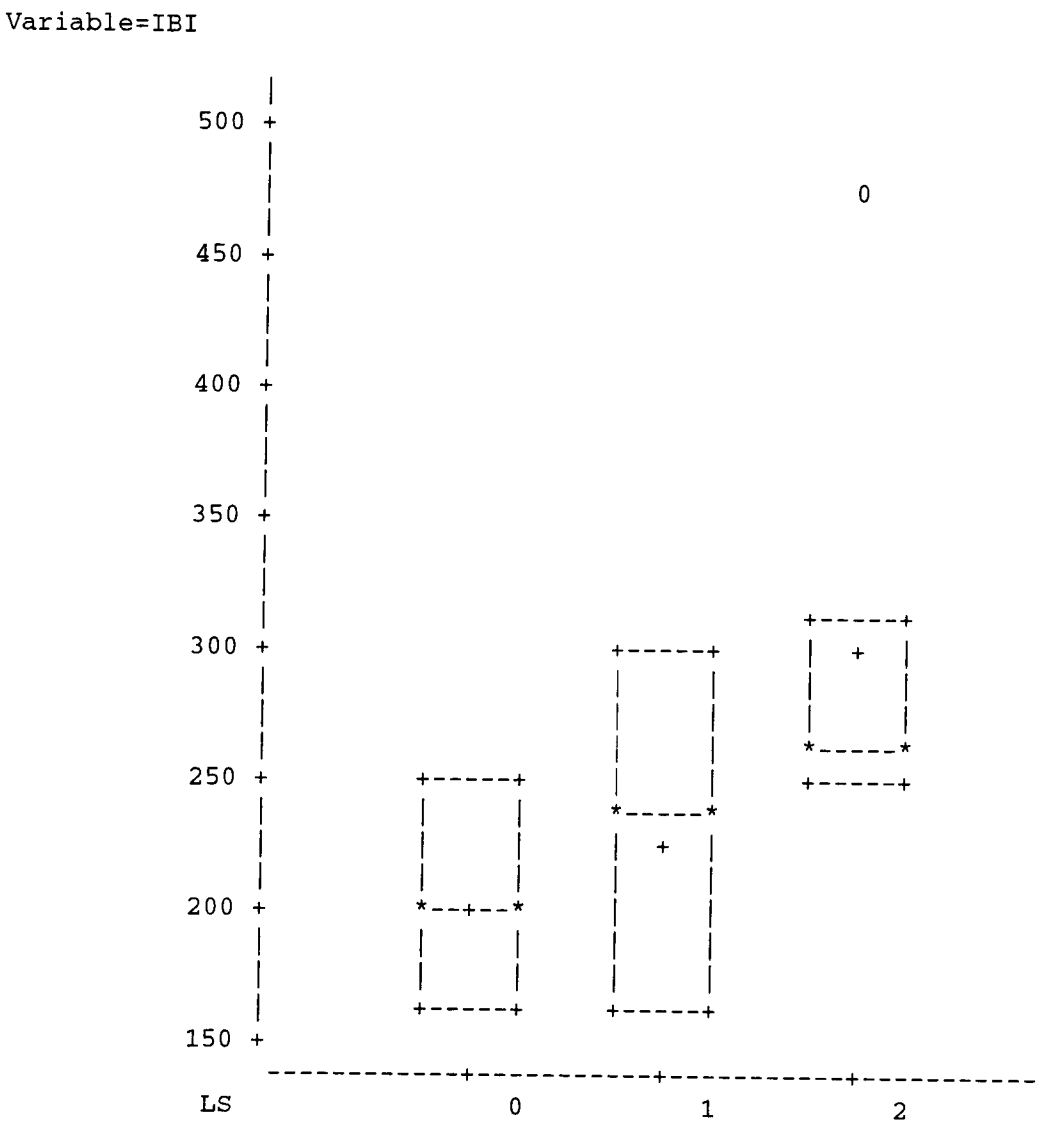


Figure 4. Analysis of Interbirth Interval by Litter Size for Oak Ridge Mothers in Poor Health. Mothers in poor health tend to have longer interbirth intervals when raising 2 infants than 1 or 0 (p =.11, N=12).

interval (p=.91, N=12), and therefore the hypothesis of reproductive depression of unhealthy mothers was not supported.

Finally, I examined the sex ratios of the offspring born at the end of the interbirth interval during which their mother was classified as ill. The offspring sex ratio of mothers in poor condition was 1.0 (11 males, 11 females, p=.58) (refer back to Table 4). The sex ratio of those offspring that survived the first month was 0.62 (5 males, 8 females, p= .29). The offspring sex ratio at birth of mothers in good condition was 0.58 (10 males, 17 females, p=.12). However, mothers in good condition raised 6 males and 13 females (sex ratio= .46, p=.08). This probability is suggestive, especially considering the similar trend in the Walters Life Science colony (see below). Colony-wide higher male mortality is unlikely as an explanation for this phenomenon (Jaquish 1993).

II. Walters Life Science colony

Demographic records from the Walters Life Science colony were also examined for comparison with the Oak Ridge data. Due to the newness of this colony, sample sizes were small. The classification of mothers for this analysis was also described in Chapter III.

The overall birth sex ratio at Walters was also skewed towards females, (9 males, 14 females, sex ratio=.64, p=.20). The birth sex ratio of lighter mothers was 1.0 (5 males, 5 females, p=.62), while the birth sex ratio of heavier mothers was .44 (4 males, 9 females, p=.13).

The sex ratio of surviving (to one month) infants of lighter mothers was .60 (3 males, 5 females, p=.36). However, the heavier mothers raised only 1 male and 5 females (sex ratio= .20, p=.11). The importance of these data is that they show the same trend that was seen in the colony at Oak Ridge, namely that mothers in better condition are more likely to give birth to and raise females than males. Fisher's method for combining probabilities (Sokal and Rohlf 1981) was therefore used to combine the samples for the sex ratio of surviving infants of good condition mothers in both the Oak Ridge and WLS colonies, with a resultant probability of p=.05. Using the sequential Bonferroni method to compute table-wide significance levels, no p-values were significant table-wide at $p \leq .05$ (Rice 1989).

An additional peculiarity of the Walters Life Science data is the low survivorship of infants born to heavier mothers. Four mothers in the demographic portion of this study delivered triplets. Three out of the four mothers were classified in the heavier category. In one case, the triplet delivery caused complications leading to a caesarian

delivery. In all four cases only one triplet survived. Litter size has low repeatability within mothers, and triplet survivorship is normally lower than that of twins (Jaquish 1991).

III. Discussion

In this chapter demographic records from the Oak Ridge and Walters Life Science colony were examined for whole colony sex ratio bias. In addition, an analysis of interbirth interval and offspring sex ratio was carried out on a subset of Oak Ridge marmoset mothers who were identified as clinically ill during their pregnancies and treated, as well as age-matched mothers who were not treated. The Oak Ridge colony was found to have a strong (though not significant at $p=.05$) bias towards female births, with the bias increasing as mothers in poor condition were selectively removed. Reanalysis at a probability of 51.5:48.5 (a slight male bias typical for a mammal) raised the significance of the Oak Ridge colony sex ratio to $p=.01$, and the other p-values accordingly. The analysis of interbirth interval revealed an effect of maternal health on interbirth interval but no effect of litter size or offspring sex ratio.

An analysis of the sex ratio of the offspring of Oak Ridge mothers in good condition, when combined with Walters

Life Science mothers in good condition, revealed a significant bias towards female offspring surviving to one month. This result is interesting for several reasons. First, it is opposite to trends seen in polygynous, sexually dimorphic mammals and as such supports the Trivers-Willard hypothesis. Also, it has management implications for the maintenance of captive colonies, in that well-maintained colonies should be expected to produce an excess of females. This may be used in retrospect to assess the health of established colonies but also necessitates careful planning for the maintenance of populations.

CHAPTER V

BEHAVIORAL ANALYSIS

I. Organization of Data

A. Categorization of Infants

Infants were placed into categories on the basis of four variables: infant sex, the condition of the mother, the condition of the infant, and the litter size. Methods for classifying mothers have previously been described. Although I planned to use weight loss or gain as a method of defining maternal health, examination of the data revealed only one biologically significant weight loss. This mother was already in the lighter or "poorer condition" category based on her absolute weight. Absolute weight therefore ended up being the criterion used for all assessments of maternal condition. Infant condition was defined at birth by weight ("small" being $\leq$ 26 g, "large" being over 29 g). This division was chosen because the infants formed two distinct groups, with no infants between being born 29.5 and 26 g, and no infants born under 25 g surviving. Condition of the infant was redefined by weight at three weeks and

again at two months. Of the two infants that were small at birth and followed for the entire four months, one remained small throughout the study and one grew to a normal size. One infant that was large at birth was classified small after 3 weeks and grew to a normal size after two months. One infant that was large at birth was placed in the small category after 2 months. All other large infants remained in that category.

B. Sample Size

The final sample size for the behavioral analysis was 13 infants (9 litters) for the first three weeks, 11 infants (7 litters) for weeks 3 to 8, and 8 infants (5 litters) for months 2 to 4 (Appendix B). Because of the small sample size, multivariate statistics could not be employed. There were multiple litters from some dams, although because of the small sample size each litter was treated independently. The behavioral sample also contained far fewer males than females (3 males to 10 females in the first 3 weeks postpartum, 3 males to 8 females for weeks 3 to 8, and 3 males to 5 females for months 2 to 4).

C. Possible Variables Confounded with Those of Interest

Several factors might be possible confounds within this sample, such as group size and maternal parity. Maternal parity was not completely confounded with maternal condition because both groups contained both primiparous and multiparous females. Group size has been shown to have no effect on a wide range of infant care parameters in this and other callitrichid species. These parameters include growth (Jaquish 1993) and mother's contribution to infant care (Tardif et al. 1990, McGrew 1988).

D. Hypotheses Addressed

Due to the sample available, questions of the effect of infant sex on maternal behavior were difficult to address. Because of the complete confounding of litter size with other variables (discussed in the next section), as well as a sample size so small that some conclusions would have been based on a single infant, I was unable to address Hypotheses 1 and 2 (predictions about the effect of infant sex on maternal behavior). To answer these questions a much larger sample size will be needed. I addressed questions about maternal and infant condition relative to maternal investment brought up in Hypothesis 3.

II. Data Analysis

Equal numbers of 30 minute observations were used for each infant. For the first 3 weeks, 23 observations were used; weeks 3 - 8, 14 observations; and weeks 8 to 16, 26 observations. These observations were distributed reasonably evenly over the time periods in question. The behaviors analyzed relative to maternal investment were infant carrying, nursing, and food provisioning. The range and distribution of these variables relative to maternal and infant conditions is presented and discussed.

A. Infant Carrying

Mothers carried singletons more than they carried twins in the first 3 weeks (Figure 5). Because of this effect, it was difficult to assess both litter sizes at the same time. I could not analyze singletons and twins separately because the samples for each were too small. Therefore, I attempted to analyze carrying relative to maternal condition only, not infant sex. This allowed me to use a combined carrying score for each litter, in the hope of more accurately reflecting the amount of weight carried by the mother.

When analyzed for the first 3 weeks and weeks 3 to 8, no relationship was found between whole litter infant



Figure 5. Total Maternal Carrying per Infant for the First 3 Weeks. The data are grouped by litter size and sex of the infant. Every singleton was carried more than every twin, and there is no apparent relationship between infant carrying and infant sex.

carrying and maternal condition (Figures 6 and 7). More information is needed in order to consider infants on an individual basis according to sex.

B. Nursing

Two scores were calculated, a minimum nursing time and a maximum nursing time. The minimum time consisted of time spent axial which was directly visible to the observer. The maximum time consisted of time in which the infant could be assumed to be nursing but was not directly observed, for instance, when the mother was in the nestbox carrying the infant and exited with it nursing. After examination of the data, I felt that the minimum nursing time unduly reflected the tendencies of certain mothers either to nurse in the nestbox or to nurse a certain infant on a non-visible side. Therefore the maximum nursing score was used in analyses.

In nursing scores the sample size was still too small to allow for the analysis by infant sex. The maximum nursing score which an infant received was analyzed according to its condition. The maximum nursing score for each litter was analyzed according to maternal condition.

For the first 3 weeks, small infants appear to have been nursed more than most large infants (Figure 8), although the ranges overlap. This relationship did not hold true in weeks 3 to 8 (Figure 9), in which the two small

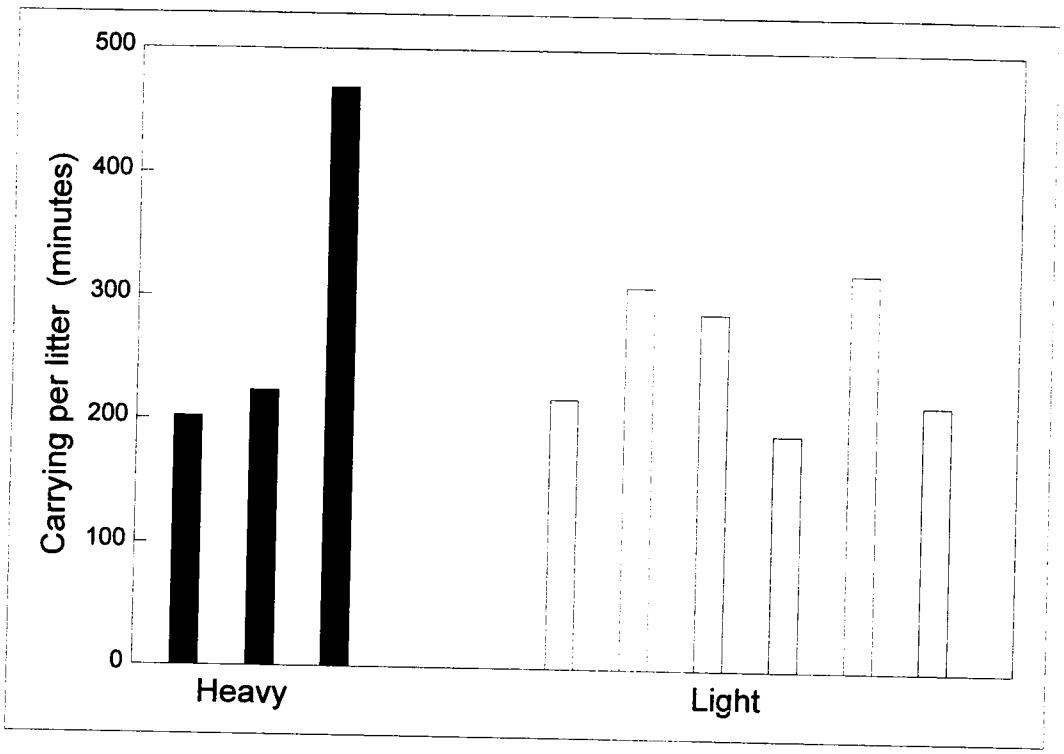


Figure 6. Total Carrying per Litter for the First 3 Weeks. The data are grouped by the condition of the mother. There is no apparent relationship between infant carrying and maternal condition in this time period.

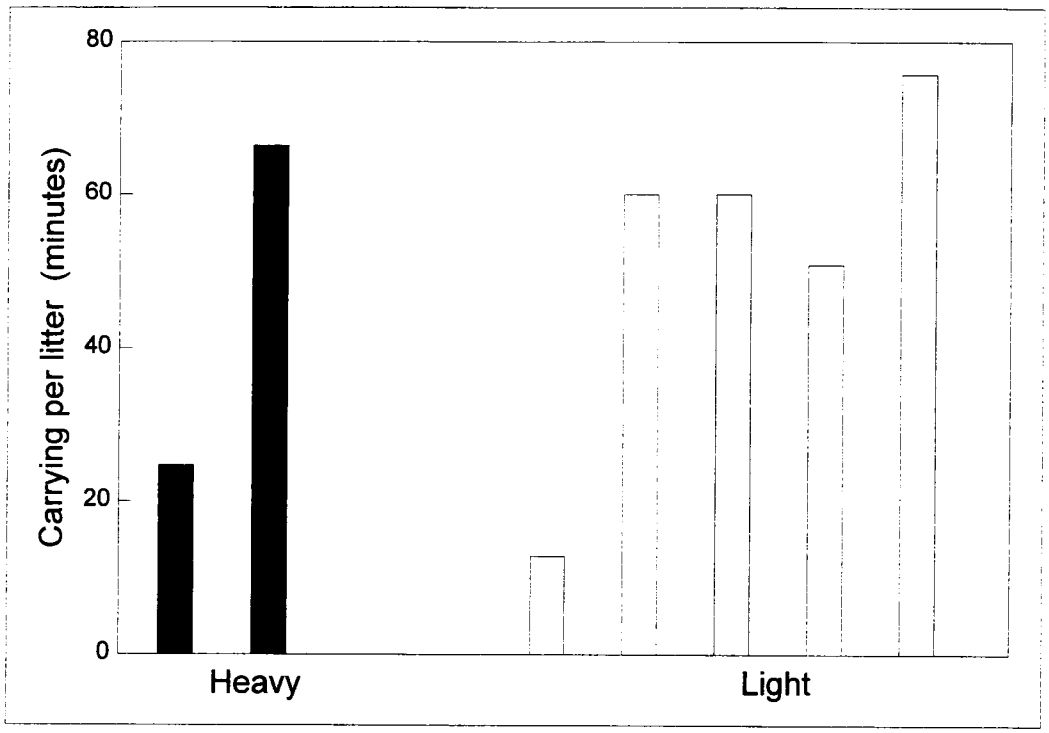


Figure 7. Total Carrying per Litter for Weeks 3 to 8. The data are grouped by the condition of the mother. There is no apparent relationship between infant carrying and maternal condition in this time period.

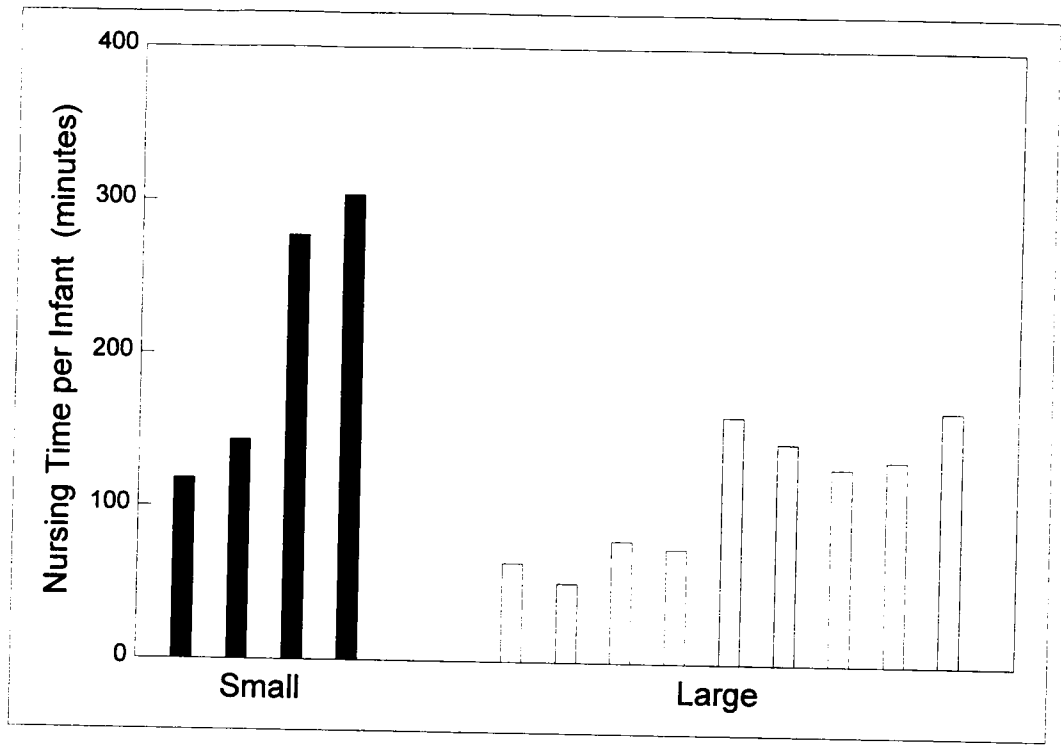


Figure 8. Nursing Time per Infant for the First 3 Weeks. The data are grouped by the condition of the infant. Although the ranges overlap, small infants appear to be nursed more than large infants.

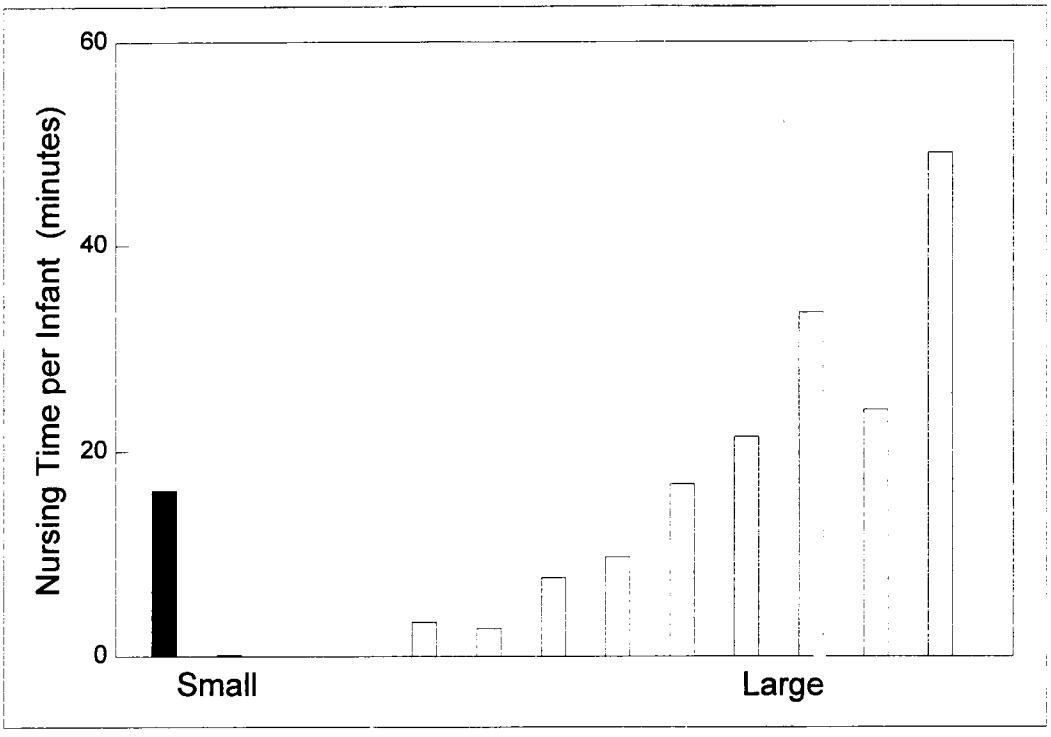


Figure 9. Nursing Time per Infant for Weeks 3 to 8. The data are grouped by the condition of the infant. Small infants are no longer nursed more than large infants, and in fact the opposite appears to be true.

infants scored in the low to middle range. This phenomenon has several explanations. The infants that were small at the age of 3 weeks may have been so because they were nursed less in the first place, in which case continued low nursing scores might be expected. It could also be that mothers were not investing in the small infants because they were small. Weeks 3 to 8 were also a period in which the infant was obtaining much food independently, which may have affected the nursing scores.

For the first 3 weeks and weeks 3 to 8, there was no apparent relationship between a mother's condition and the amount of nursing which she invested in her entire litter (Figures 10 and 11). It is possible that the mother was responding more to cues from the individual infants than to her own condition.

C. Food Provisioning

By months 2 to 4, carrying and nursing behaviors occurred only in very low frequencies and were usually resisted by the parent. The only behavior analyzed for this time period was food provisioning of the infant by the mother. This was analyzed as time eating food shared by the mother per beg of the infant. As defined earlier, this involved the infant begging for food and receiving it from

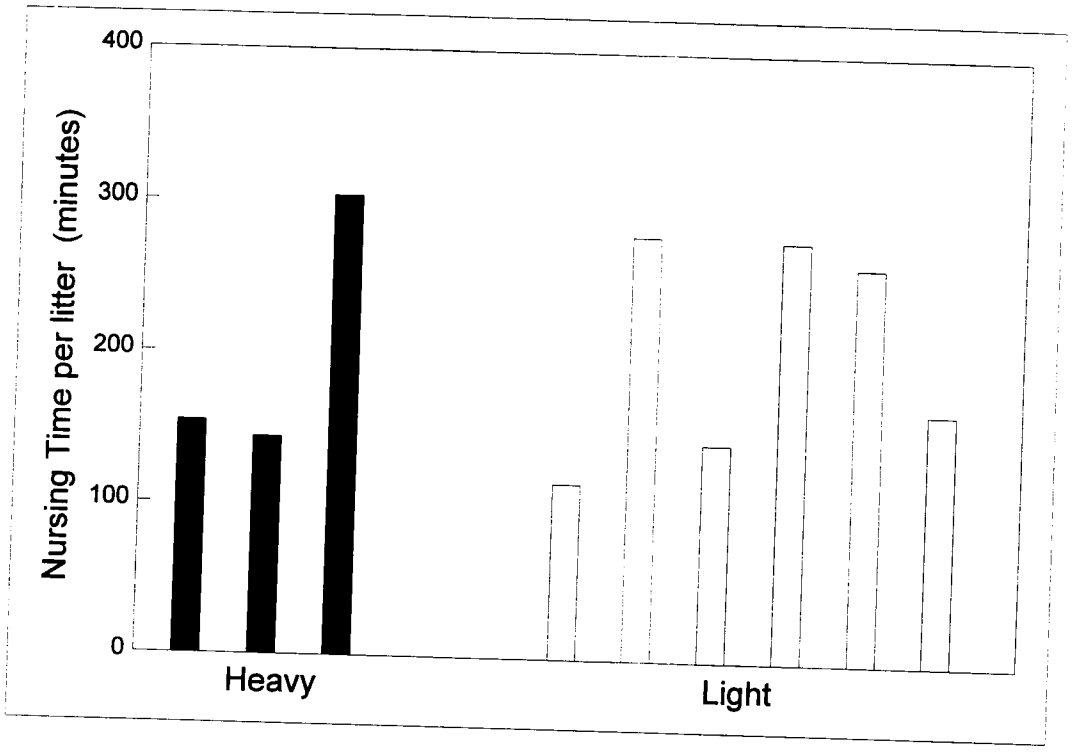


Figure 10. Nursing Time per Litter for the First 3 Weeks. The data are grouped by the condition of the mother. There is no apparent relationship between the condition of the mother and the amount of nursing invested in each litter.

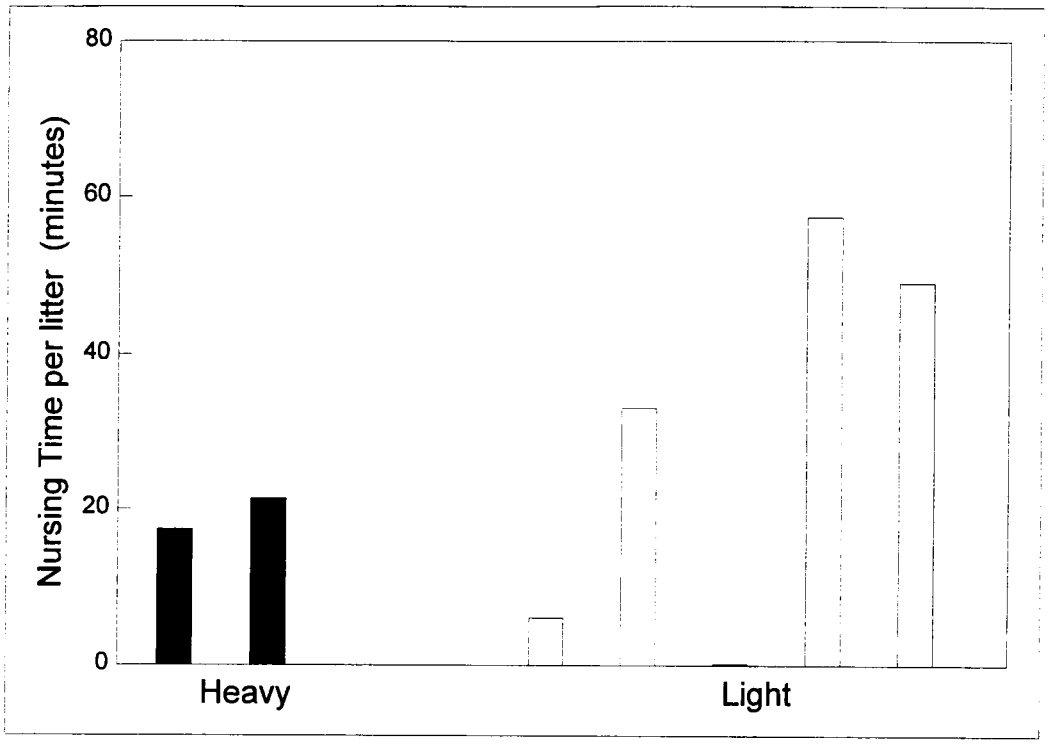


Figure 11. Nursing Time per Litter for Weeks 3 to 8. The data are grouped by the condition of the mother. There is no apparent relationship between the condition of the mother and the amount of nursing invested in each litter.

the mother with no resistance within ten seconds. For this particular behavior, singletons did not receive higher investment than twins. All infants were therefore considered individually and as entire litters while exploring the relationship between food provisioning and infant and maternal condition. Individual infants' percentage of begs successful and amount of provisioning per successful beg are available in Table 5. Data used in analysis included both successful and unsuccessful begs.

The most interesting result from this analysis is that most heavy mothers provisioned their infants more than most light mothers (Figure 12). This result was the same both when infants were considered individually and when whole litters were examined.

The one infant to a light mother that scored very high was anomalous in several different ways. This subject (Infant #51) was a son of a light mother. Although he had a fairly high begging rate (14 times in the 2 month period), it was not the highest begging rate. His female twin, which begged a similar amount (10 times), received considerably less food per beg through provisioning (27.5 s of provisioning/beg versus 8.8 s/beg). Male #51 was not particularly small at birth (29.5 g, range = 25.0 g to 33.5 g). At 3 weeks he was still of normal weight (51.0 g, range= 43.87 to 53.1 g). However, by 2 months of age he was the smallest infant in the study at 84.1 g (mean= 109.7 g,

Table 5. Food Provisioning of Infants, Months 2 to 4.

Infant Number	Percentage of Begs Successful	Mean ± s.d. for successful begs (s)
44	0	None
45	13%	30.5 ± 30.4
49	82%	27.3 ± 26.6
50	82%	21.8 ± 16.2
51	79%	35.0 ± 30.3
52	40%	22.0 ± 22.2
54	50%	14.1 ± 9.7
56	50%	34.8 ± 13.8

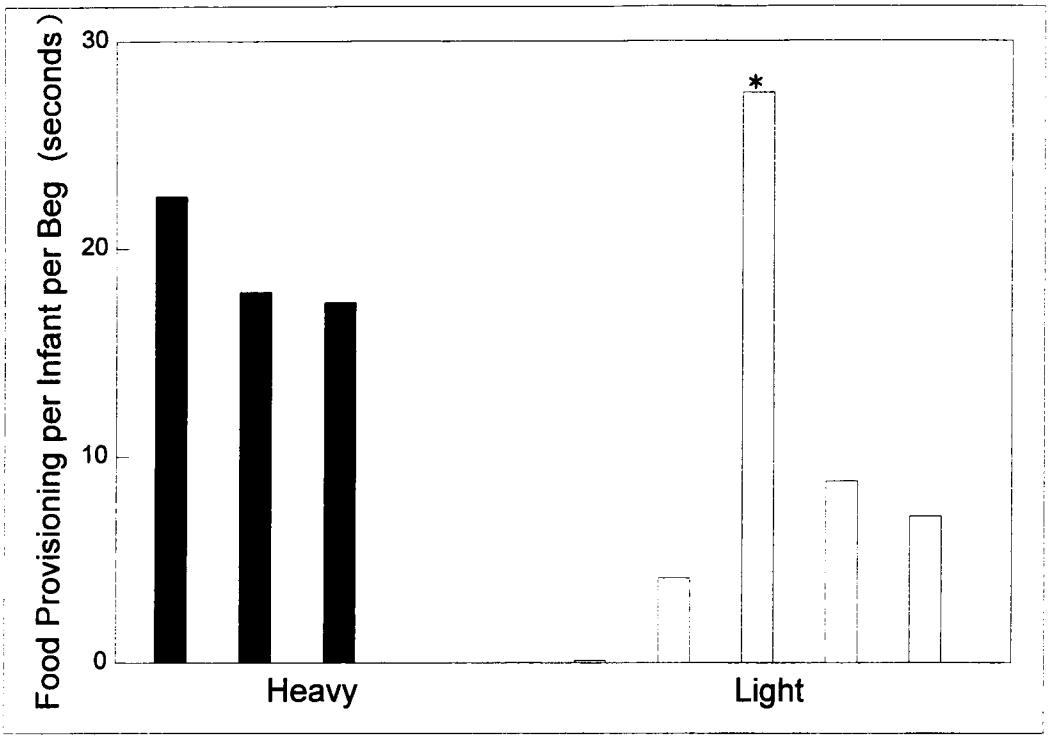


Figure 12. Food Provisioning per Infant per Beg, Months 2 to 4. The data are grouped by the condition of the mother. Most infants of heavy mothers are provisioned more per beg than most infants of light mothers. The data point marked with an asterisk (*) is discussed in the text.

range= 84.1 g to 134.0 g). One possibility is that this infant was less behaviorally developed than the other infants in the study and was taking less food independently. In fact, his total eating score, which measured total food eaten minus that from maternal sharing, was the lowest in the study for weeks 3 to 8 (his score = 231 s, mean = 501 s). During months 2 to 4 he did not have the lowest eating score but was below average (his score = 1342 s, mean = 1867 s). #51 was also observed anecdotally to display delayed pelage development, which may be linked to delayed behavioral development (Tardif, personal communication).

The condition of the infant (small or large) did not appear to have an effect on the amount of food provisioning it received (Figure 13). As discussed above, the very high-scoring small infant may have been anomalous. In addition, the only other infant that was still small at 2 months of age also displayed behavioral anomalies. She was off carriers very early, and a young infant off carriers may sustain an energy deficit due to the demands of thermoregulation (Jaquish 1993). Also, when transferred from carrier to carrier, rather than stopping her distress calls and assuming a dorsal position near the neck like most infants, she often continued to cry and remained ventral on the carrier. This often led to her immediate harassment and transfer to either another carrier or the cage wall. In summary, infants in this study that were small at 2 months

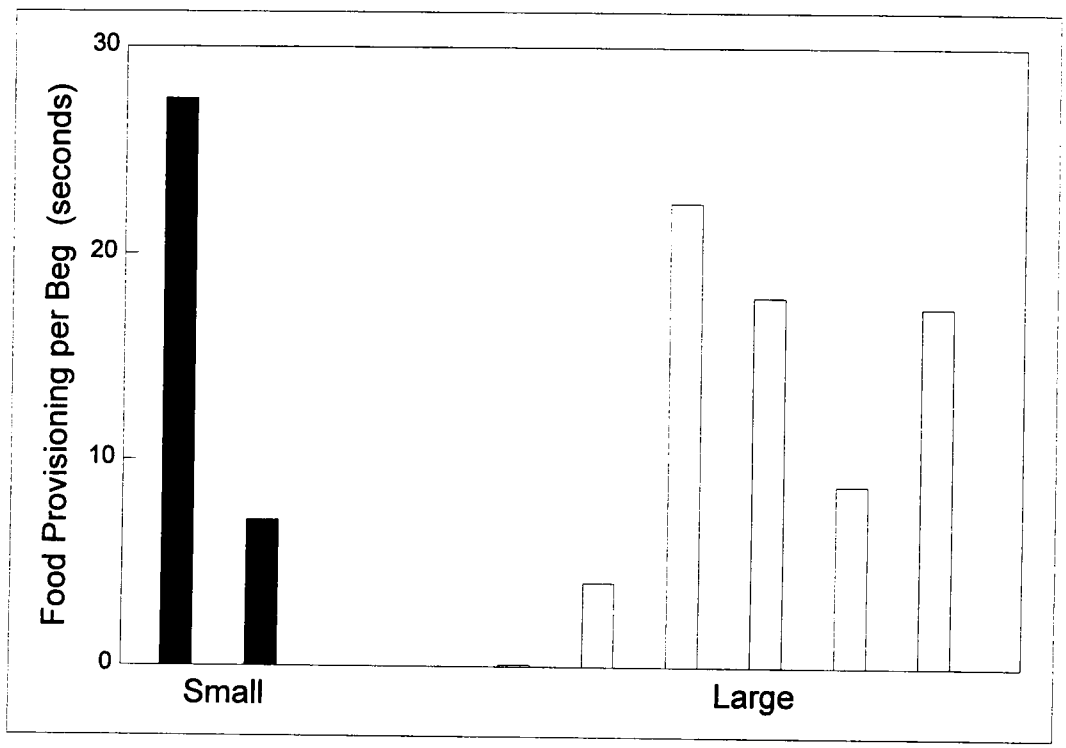


Figure 13. Food Provisioning per Infant per Beg, by condition of infant. The data are grouped by the condition of the infant. There is no apparent relationship between the size of the infant and the amount of food provisioning it received. The two small infants are both discussed in the text.

displayed behavioral abnormalities which may have affected the amount of provisioning they received.

III. Summary

The behavioral data in this study must be analyzed qualitatively because of small sample size and infant categories with no representation. Statements which can be made about this data are:

1. Singleton infants were carried more by the mother than twins throughout the first two months of life. Most singleton infants were nursed more than most twins for the first three weeks, although this trend was not complete and did not carry through weeks three to eight.

2. There was no apparent relationship between the condition of the mother and the amount of total infant carrying by her per litter for the first 3 weeks or weeks 3 to 8.

3. Most small infants were nursed more for the first 3 weeks than most large infants, although this did not hold true for weeks 3 to 8. There was no apparent relationship between the size of the mother and the amount of nursing per infant.

4. Litter size was no longer significant when considering food provisioning from 2 to 4 months. In general, heavy mothers provisioned infants more per beg and light mothers provisioned infants less. Behavioral differences on the part of the infant are a possible explanation. No relationship was observed between infant size and food provisioning per beg.

Because of the small sample size, I was unable to explore the relationships between infant sex and maternal condition predicted in Hypotheses 1 and 2. Hypothesis 3, which predicted higher investment in larger infants, was not supported in the data for nursing for the first 3 weeks, and in fact the opposite was seen. However, it is notable that the smaller infants which received very high investment were both singletons; the mother had only one infant available for investment, and was without the alternative of transferring investment to another infant in the same litter. For weeks 3 to 8, the predicted relationship between the size of the infant and the amount of nursing was seen.

The results predicted by Hypothesis 3 were also supported by the data on food provisioning, in that heavy mothers provisioned more and light mothers provisioned less. However, there was no relationship between food provisioning

per beg and the size of the infant, which was also predicted by Hypothesis 3.

One subject which must be addressed is the effect of unequal numbers of repeated measures on different dams. Some mothers certainly invested much more highly in their offspring than others. However, one mother showed very different investment patterns between twin offspring; she carried, nursed, and provisioned the male infant more than the female. Another mother showed very different patterns between each of her three litters; investing very little in her first set of twins even when their scores were combined; very little in her next litter, which was a singleton, compared to other singletons; and then highly in her third litter, which was another singleton. More information is needed to assess the effect of maternal identity, but it does not appear to invalidate the results obtained.

Although these data are very preliminary and not extensive enough for multivariate analysis, they do suggest that exploration of the effect of infant and maternal condition on parental investment may be worth pursuing. Post-natal maternal behavior may eventually lend clues to the trends seen in the demographic data.

CHAPTER VI

DISCUSSION AND CONCLUSIONS

Parental investment and sex ratio theory are, like most sociobiological topics, controversial and far from fully explored. Different definitions and measurements of variables have added to the confusion. This study has attempted to assess parental investment in a polyandrous, communal-care primate, the common marmoset. Strong evidence was found from demographic records that marmoset mothers in good condition have birth sex ratios biased towards daughters. In addition, their infants surviving to one month, when compared across samples, tend to be biased towards daughters. Preliminary behavioral evidence also suggests that maternal and infant condition have an effect on maternal investment. In the case of nursing time of infants up to the age of 3 weeks, however, this effect was in the direction opposite to that predicted.

How do these findings support or refute the Trivers-Willard hypothesis and current sex ratio theory? One test of the robustness of any hypothesis is whether or not it stands up in situations different from, or opposite to, that in which it was originally tested. Most previous sex ratio studies were carried out in polygynous, sexually dimorphic

species with large male variances in reproductive success. The common marmoset is polyandrous and sexually monomorphic, with a large female reproductive variance. The fact that, at least demographically, the Trivers-Willard hypothesis works in reverse is a strong argument in its favor. In addition, this bias is the opposite of the norm and appears to be operating contrary to any suggested mechanism of sex ratio adjustment. Female-biased birth sex ratios are very uncommon among mammals, with some species of lemmings being one of the few exceptions (Clutton-Brock 1982). As discussed in Chapter II, neither pre-conception hormonal hypotheses or pre-natal differential harassment could be used to explain an excess of female births. This departure from normality is another valuable indicator because of its counterintuitiveness but consistency with the hypothesis.

One matter that should be addressed is the feedback between maternal and infant behavior. As mentioned previously, some apparently inconsistent results can be partially explained by differences in the infant's behavioral development. A body of theory exists on parent-offspring conflict (Redondo et al. 1992, Gomendio 1991), which predicts that each offspring should try to extract a level of investment which maximizes its own fitness, while a parent should cut off investment in one offspring at some point to invest in the next offspring and maximize the parent's lifetime fitness. An infant who demonstrates a

higher rate of begging or crying may extract higher investment than one who does not. In addition, behavioral anomalies of the infant can affect parental investment either to raise or lower it. Both maternal and infant characteristics should be examined.

What are some directions for future study? An important step in any future sex ratio study is the quantification, as accurately as possible, of maternal investment ability. Measurement of maternal fat reserves would be preferable, or maternal weight if these are not available. In addition, reproductive variance of species being studied should be quantified rather than assumed.

The proximate mechanism for sex ratio variation is also largely unexplained. Physiology, behavior and demographics are all intertwined and the absence of a known mechanism hinders the exploration of sex ratio adjustment as a possible adaptive mechanism.

Continued data collection on captive animals is needed and will allow for the control of situations such as retrieving stillbirths and close monitoring of maternal condition, as well as leading to better management of captive populations through understanding of their population structure. Data collection in free-ranging populations will allow us to avoid assumptions made when working with captive populations, give more meaning to the idea of resource competition, and lead to a better

understanding of the demographics and population dynamics of the species involved, ultimately improving attempts at conservation. In addition, other species which might lend themselves to predictions different from those normally made, by both the Trivers-Willard and local resource hypotheses, should be studied. Among primates, this might include not only callitrichid species, but monogamous, monomorphic species such as gibbons or saki monkeys, in which no sex ratio adjustment would be expected; prosimians, which have varied and unusual social structures and have hardly been examined at all; and species with male philopatry and female transfer, such as chimpanzees and red colobus monkeys. Exploration of this topic is promising but still has far to go.

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APPENDIXES

APPENDIX A. AGE-MATCHED OAK RIDGE FEMALES USED IN ANALYSIS OF INTERBIRTH INTERVAL

Poor Condition	Good Condition	Age
5209	5665	6 yr 11 mo, 6 yr 10 mo
5213	4726	5 yr 3 mo, 5 yr 1 mo
5221	5219	4 yr 7 mo, 4 yr 1 mo
5237	5677	3 yr 6 mo, 3 yr 6 mo
5251	5657	6 yr 4 mo, 6 yr 5 mo
5263	5000	4 yr 7 mo, 4 yr 8 mo
5265	5659	3 yr 1 mo, 3 yr 1 mo
5271	4752	4 yr 10 mo, 4 yr 5 mo
5281	5267	8 yr 8 mo, 8 yr 6 mo
5285	5287	8 yr 9 mo, 8 yr 9 mo
5397	5687	3 yr 11 mo, 3 yr 11 mo
5649	5412	3 yr 6 mo, 3 yr 5 mo
5655	5447	6 yr 1 mo, 6 yr 1 mo

APPENDIX B. FAMILY COMPOSITION OF GROUPS USED IN BEHAVIORAL ANALYSIS

Infant	Dam	Sire	Birthdate	Time observed	# of Siblings
44	018	019	5/11/94	4 months	1 twin, 3 older
45	018	019	5/11/94	4 months	1 twin, 3 older
49	028	029	8/02/94	4 months	1 twin, 5 older
50	028	029	8/02/94	4 months	1 twin, 5 older
51	003	012	10/02/94	4 months	1 twin, 2 older
52	003	012	10/02/94	4 months	1 twin, 2 older
54	018	019	10/12/94	4 months	5 older
56	002	010	12/11/94	4 months	None
61	001	034	3/12/95	3 weeks	None
62	003	012	3/14/95	2 months	1 twin, 4 older
63	003	012	3/14/95	2 months	1 twin, 4 older
64	018	019	3/25/95	2 months	6 older
67	024	009	5/7/95	3 weeks	None

VITA

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