



Explaining variation in maternal care in a cooperatively breeding mammal

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Because of the necessity of lactation, mammalian mothers must perform at least a minimum amount of infant care. In cooperatively breeding species, other group members aid in all other aspects of infant care. However, some mothers continue to carry and nurse their infants more than others. The golden lion tamarin, *Leontopithecus rosalia*, is a small, communally breeding primate in the family Callitrichidae. We studied hormonal, individual, historical and social factors hypothesized to contribute to variation in levels of maternal care. We used neonatal weight as a measure of prenatal care, and carrying and nursing as measures of postnatal care. Greater neonatal weight was associated with smaller litter size, lower prepartum levels of oestrogen conjugates, and higher prepartum cortisol levels. Higher rates of carrying during weeks 2 and 3 were associated with higher maternal weight, larger litter size and smaller numbers of helpers per infant. Higher rates of nursing in weeks 2 and 3 were predicted by smaller group size and provisioning of the mother. The most important factors affecting postnatal maternal care were maternal weight, group size, litter size and provisioning status of the mother. Thus, females that display higher levels of maternal care do so either because they have to (they have fewer helpers) or because they can (they are in better condition).

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Maternal care in mammals differs from that of other vertebrates in that the sole source of nutrition for new infants is lactation, and thus the mother is obligated to provide a certain minimum amount of care to her infants (Clutton-Brock 1991). The level of maternal care given by an individual mother may vary according to such factors as maternal age (horses, *Equus caballus*: Cameron et al. 2000), offspring litter size (roe deer, *Capreolus capreolus*: Anderssen & Linnell 1997), and maternal condition (big-horn sheep, *Ovis canadensis*: Festa-Bianchet & Jorgensen 1998). Furthermore, the sex of the offspring (or sex ratio of the litter) may influence maternal care, since mammalian mothers often invest more in male infants than in females (review in Clutton-Brock & Iason 1986). Although it is unlikely that the many factors that affect levels of maternal care act independently, they are rarely considered simultaneously for any species.

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In cooperatively breeding mammals, all forms of offspring care except nursing can be provided by other group members. Thus, a second question arises: why does a mother provide more care than absolutely necessary, when other group members could provide the difference? Literature on mammalian cooperative breeders often focuses on the level of care provided by the father and alloparents (Mitani & Watts 1997; Solomon & French 1997), rather than the mother. Research on the mother has focused on the effect of variation in the number of helpers on her level of parental care, and/or the impact of that care on offspring survival (dwarf mongooses, *Helogale parvula*: Creel & Waser 1994; black-backed jackals, *Canis mesomelas*: Moehlman 1979; captive marmosets and tamarins (Family Callitrichidae): Pryce et al. 1988; Tardif et al. 1990; Price 1991; Jaquish et al. 1997; Santos et al. 1997; wild marmosets and tamarins: review in Heymann & Soini 1999; Bales et al. 2000). Other studies have examined maternal care measured as energetic costs of infant care, either in terms of weight loss (Sánchez et al. 1999) or incompatibility with other behaviours (Price 1992b; Tardif & Bales 1997). With the exception of group size and dominance status (Dietz & Baker 1993; Digby 1994), factors that can potentially influence levels of maternal care in

wild populations of cooperatively breeding primates are largely unstudied.

Variation in maternal care is probably mediated by a complex suite of variables, including endocrine-mediated differences, and historical, individual and social effects on maternal care. Although the role of hormones in maternal care is well established for some mammals (Poindron & Lévy 1990; Rosenblatt 1990; Bridges 1996), until recently it was maintained that maternal hormone levels did not impact maternal care in primates (Coe 1990; Keverne et al. 1997). Recent work in both Old World and New World primates is challenging this view. Levels of prepartum oestrogen and the hormonal conditions of late pregnancy have been linked to maternal responsiveness in pigtailed macaques, *Macaca nemestrina* (Maestripieri & Wallen 1995; Maestripieri & Zehr 1998), as well as infant survival levels in red-bellied tamarins, *Saguinus labiatus*, and common marmosets, *Callithrix jacchus* (reviews in Pryce 1993, 1996; see also Fite & French 2000). In humans, high levels of maternal cortisol are related to a mother's attraction to her own infant and her ability to recognize her own infant (Fleming et al. 1997b). In addition, patterns of change in oestradiol/progesterone ratios are related to a mother's postpartum attachment feelings for her infant (Fleming et al. 1997a).

In addition to these proximate physiological factors, prior infant care experience, parity, litter size, condition and group size are also known or hypothesized to affect maternal care in callitrichids (review in Snowdon 1996). Of these, prior infant care experience is perhaps the best studied. Lack of helping experience, as well as primiparity, reduces the adequacy of infant care (Hoage 1977; Tardif et al. 1984; French et al. 1996). In captive callitrichids, litter size affects levels of maternal care (singletons are carried more than twins; Price 1991, 1992a; Tardif et al. 1990, 1993), and maternal body weight affects the number of eggs ovulated (Tardif & Jaquish 1994, 1997). In other primates maternal condition affects the level of postnatal maternal care (Fairbanks & McGuire 1995; Lee 1987). In golden lion tamarins, *Leontopithecus rosalia*, mothers at higher body weights give birth to larger litters (Bales et al. 2001). In most callitrichids, as group size (and therefore number of helpers) increases, paternal effort decreases but maternal effort does not (review in Bales et al. 2000). Interactions among maternal condition and other factors such as the sex of the infant may also be important in determining levels of maternal care, especially if maternal care affects lifetime reproductive success of the sexes differently, as per the Trivers-Willard hypothesis (Trivers & Willard 1973; review in Clutton-Brock & Iason 1986). In this study, we examined the effects of multiple variables on levels of maternal care in a cooperatively breeding primate, the golden lion tamarin.

METHODS

Site and Subjects

Subjects for this study were 16 female tamarins, 11 that were native to Poço das Antas Biological Reserve (PDA)

and five located in reintroduction areas, with a total of 37 infants. PDA is situated in a fragment of the Atlantic Coastal Forest of Rio de Janeiro State, Brazil. Drs James Dietz, Andrew Baker and colleagues have maintained a long-term study of this population since 1983, and maintain a sample of 20 groups in which all individuals are tattooed and dye-marked. At least one animal in each group is radiocollared to facilitate location.

The reintroduction areas are located on farms near PDA and are populated by descendants of captive-born individuals reintroduced from zoos (Beck & Martins 1998). The five females from reintroduction areas that were used in this study were all born in the wild and provisioned three times a week; we will refer to them as provisioned females. Descendants of reintroduced monkeys generally behave like native, wild tamarins, and are capable of independent foraging (Beck & Martins 1998). However, the continuing programme of provisioning (maintained primarily for monitoring purposes) has resulted in higher female weights than in the wild population, at least for the sample of females in this study (K. Bales, unpublished data). In addition, provisioned tamarins display lower rates of foraging, locomotion and feeding (Stoinski 2000).

Golden lion tamarins give birth to one or two litters a year and have a fertile postpartum oestrus (Wilson 1977; Dietz et al. 1994). They normally give birth to twins, who begin eating solid food at 3 weeks and are weaned at approximately 3 months (Baker 1991). The first and largest birth peak is in October–November and the second in February (Dietz et al. 1994). An analysis of weights across time showed that females do not lose weight during the infant care period (Dietz et al. 1994).

Infant Handling

Mothers and infants were noninjuriously trapped as soon as possible after birth. At this time, infants were sexed, weighed and marked with Nyanzol dye. Neonatal weights were collected on 19 infants. Neither mothers nor infants were anaesthetized during handling. We did not observe any harmful consequences of trapping. If trapping was unsuccessful, infants were marked with Nyanzol dye squirted from a syringe. To minimize the possibility that dye would enter the animal's eyes, we attempted this procedure from very short distances and only when the animal's back was to the researcher.

We defined litter size as the number of infants in the litter during the majority of the behavioural observations, not the litter size at birth (except for the analysis of neonatal weight). The mother's condition was defined as her nonpregnant body weight. In common marmosets, a closely related species, body weight is highly predictive of both fat-free and fat mass (Tardif & Jaquish 1997). We used a battery-powered scale baited with a banana to collect weights in the forest during the first month after the birth of the infant, a technique that we validated in the laboratory. Female body weights ranged from 538 to 683 g. No females were in visible ill health or malnourished, although one particularly old female (Female 3) died soon after the conclusion of this study, presumably

Table 1. Females included in study and numbers of faecal samples from each female

Female ID	Birthdate	Number of litters	Number of baseline samples	Number of third trimester samples
3	1 Sept 1981	1	8	12
291	13 Sept 1988	2	37	29
436	25 Nov 1991	2	37	29
524	4 Oct 1993	1	10	13
539	15 Nov 1993	1	11	11
603	30 Sept 1994	2	22	20
629	1994	1	3	3
651	1993	1	17	13
672	1993	1	3	8
703	1995	1	18	10
721	1994	1	16	25
CM11	Nov 1992	2	14	6
CM13	Nov 1993	1	5	7
MA9	Oct 1995	1	3	7
ST6	Mar 1993	2	21	9
ST11	Oct 1995	1	*	*

Where only the year is given, we estimated female age to within a year.

*This female was not included in hormone analyses due to lack of samples.

from old age. We defined a mother's parity as either primiparous or multiparous.

Collection, Extraction and Assay of Faecal Samples

We collected faecal samples intensively during four periods: June–July 1996 (preliminary data), June–November 1997, July–December 1998 and February–March 1999. As most births occur in October and November, these sampling periods allowed for collection during entire pregnancies for most females. During these periods, we collected samples from each female at least twice a week. We followed the animal until she defecated naturally. We froze the samples at $\approx 18^\circ\text{C}$ until analysis. Table 1 details the females in the study, their ages, and the number and distribution of samples collected from each. Numbers of samples differ between females due to circumstances such as deaths, formation of new study groups, and an unexpected birth in one subordinate female.

We allowed faecal samples to thaw at room temperature, and placed 0.125-g fractions of each sample in a round-bottom, 20-ml test-tube. We removed seeds, leafy material, and insect parts from the faecal sample prior to weighing. We added a 5.0-ml volume of solubilizer (40% methanol: 60% phosphate buffered saline (PBS)) and placed the tubes on a shaker rack overnight (12–16 h). We pelleted the particulate matter in the resulting slurry by centrifugation for 15 min at 2000 g, and separated the supernatant into a clean test-tube. We refroze the extracted samples and stored them prior to assay.

We validated faecal EIAs using urine from a captive female golden lion tamarin (French et al., in press). The particular metabolites were chosen based on previous work on captive golden lion tamarins (French & Stribley 1985, 1987; Monfort et al. 1996), and tufted-ear marmo-

sets, *Callithrix kuhli* (Smith & French 1997). Running individual females in lots minimized the effects of interassay variation.

Pregnanediol-3-glucuronide (PdG)

We assessed PdG levels by a PdG EIA previously characterized (Munro et al. 1991) and validated for golden lion tamarin faecal samples (French et al., in press). We further diluted the extracted faecal samples with assay buffer (1:5) prior to measurement to place the sample concentration within the range of the standard curve. PdG standards (Sigma Chemical Co., St Louis, Missouri, U.S.A.) ranged from 10 000 to 78 pg/well in halving concentrations. We added PdG-horseradish peroxidase (HRP) conjugate to the wells. After a 2-h incubation, we washed the plates and added hydrogen peroxide and ABTS (2,2'-Azino-bis(3-thylbenzthylolone-6-sulfonic acid)) as a chromogen. We measured absorbance at 410 nm (reference 570 nm) in a Dynatech MR5000 microplate reader, and calculated the sample concentrations using a four-parameter sigmoidal curve fitting function. Intra- and interassay coefficients of variation for high and low concentrations of a faecal quality control pool were 10.9 and 23.9% (high; $N=20$) and 7.6 and 23.7% (low; $N=20$), respectively.

Oestrogen conjugates (E_1C)

We measured faecal oestrone conjugates (E_1C) by an E_1C EIA also previously characterized (Shideler et al. 1990; Munro et al. 1991) and validated for the golden lion tamarin (French et al., in press). We diluted extracted faecal samples with assay buffer (1:20) prior to measurement to place the sample concentration within the range of the standard curve. E_1C standards (oestrone-3-glucuronide, Sigma Chemical Co.) ranged from 400 to

6.2 pg/well in halving concentrations. We added E₁C-horseradish peroxidase (HRP) conjugate to the wells. We measured absorbance 1 h later as per the PdG assay. Intra- and interassay coefficients of variation for high and low concentrations of the faecal quality control pool were 7.0 and 18.9% (high) and 5.0 and 22.5% (low), respectively.

Cortisol

We measured faecal cortisol using a cortisol EIA also previously characterized (Smith & French 1997). We coated microtiter plates (Nunc Maxisorp F96) with rabbit anticortisol (R4866) diluted 1:12 000 in carbonate coating buffer. We further diluted extracted faecal samples with assay buffer (1:10) prior to measurement to place the sample concentration within the range of the standard curve. We diluted cortisol standards (ICN Biomed, Costa Mesa, California, U.S.A.) in a 1:10 dilution of extraction buffer. Cortisol standards ranged from 1000 to 7.8 pg/well in halving concentrations. We diluted cortisol-horseradish peroxidase (HRP) conjugate (batch 11/94) 1:20 000 in PBS and added it to the wells. After a 2-h incubation, we washed the plate wells and added hydrogen peroxide and ABTS as a chromogen. We measured absorbance 1 h later as per the assays for PdG and E₁C.

We determined the precision of the faecal EIAs using the faecal quality control pool. Intra- and interassay coefficients of variation for high and low concentrations of the faecal quality control pool were 6.7 and 13.6% (high), and 6.1 and 16.0% (low). Cortisol standards and serial dilutions of extracted faeces collected from females at different times during pregnancy produced parallel displacement curves. We determined the accuracy of the assay by spiking the supernatant of a faecal sample with 100 pg of cortisol standard. The recovery of cortisol standard was $101 \pm 2.0\%$ ($N=6$).

Sample Classification and Choice of Measurements

We classified samples by trimester by counting back from the birth date of infants (based on a 132-day gestation period; Kleiman 1977). Infants were first seen either on the day of birth or the day after, so an error of 1 day is possible. To correct for individual variation in hormone levels, we used the difference between third trimester levels and nonpregnant (baseline) levels for E₁C and cortisol. We defined the baseline level as any period during which the female was not pregnant. In addition, we calculated E₁C/PdG ratios for each sample from the last 2 weeks of each female's pregnancy. We then averaged these ratios to calculate a mean ratio for the last 2 weeks prepartum.

Behavioural Data Collection

We chose to study behaviour during the first 3 weeks of life because during this period infants depend completely

on the mother for nutrition (Baker 1991). We collected a total of 154 h of behavioural data using continuous focal animal sampling on infants. We observed each infant approximately three times a week for 1–2 h each time. We observed infants for 10-min focal periods; in groups with more than one infant, we alternated focal periods between infants. We collected behavioural data between 0600 and 1500 hours. We divided the day into early morning, late morning and early afternoon, and balanced time of day roughly across mother–infant pairs; however, provisioned mothers were less likely to be observed in the early morning because of their greater distance from the main study site. We located groups by radiotelemetry. All groups were completely habituated to human observers and animals were visible over 93% of the observation time. We recorded all behaviours of the focal infant and its carrier on audio tape. In this paper we consider only the behaviours 'carry' and 'time on nipple', as they are the predominant infant care behaviours during the first 3 weeks of life. We measured these behaviours per infant. We defined an individual as carrying when it was supporting the infant's weight and at least two of the infant's limbs were clinging to the individual. We estimated time on nipple by the amount of observed time that an infant's head was axial (in the mother's armpit). To estimate time on nipple during periods when the infant was on the mother but its head was not visible to the observer, we calculated the percentage of time on nipple when infants were completely visible, not crying, and the mother was still. This amount was $\approx 63\%$ of observation time. Infants were therefore assumed to be on the nipple for 60% of time spent nonvisible, on the mother, and not crying (this occurred in approximately 1.3% of the total observation time).

Data Analysis

The variables used in all models are listed in Table 2. We transformed non-normal data to normality using the arcsine square-root transformation. We analysed the data by generalized linear mixed models (Diggle et al. 1999), using Proc Mixed in SAS Version 6.0 (SAS Institute, Cary, North Carolina, U.S.A.). We incorporated the infant's mother and the litter within mother into the model as random factors, thus solving the problem of pseudoreplication by accounting for correlations within the data. If both of these random effects were dropped from the model, we performed a standard linear regression. We chose fixed effects by backward selection, and considered $P < 0.05$ statistically significant. Maternal carrying during the first week was not transformable to normality due to the substantial number of mothers that carried their infants 100% of the time. We therefore divided mothers into those that carried at least 50% of the time and those that carried less than 50% of the time. We then analysed these data by the GLIMMIX macro (Littell et al. 1996), which allows for random effects in a logistic model. Relationships between explanatory variables were explored using Pearson's correlation coefficients. Values reported are means \pm SE.

Table 2. Variables used in mixed models

Dependent variable	Independent variables
Neonatal weight	Infant age at weighing (covariate) Litter size Maternal body weight Condition*litter size Infant sex Sex of infant*condition of mother Maternal age Oestrogen conjugates Cortisol Oestrogen/pregnanediol Mother (random) Litter (mother) (random)
Nursing, week 1	As above (except for infant age) and below
Nursing, weeks 2 and 3	
Carrying, week 1 (at least 50% versus less than 50%)	Helpers per infant (group size)
Carrying, week 2	Maternal parity

RESULTS

Relationships Between Explanatory Variables

Significant correlations existed between E₁C and cortisol (Pearson correlation: $r_{27}=0.49$, $P<0.01$); cortisol and maternal body weight ($r_{27}=0.44$, $P=0.02$); provisioning and E₁C levels, with provisioned animals having higher E₁C ($r_{27}=0.44$, $P=0.02$); and maternal age and maternal body weight ($r_{27}=-0.46$, $P=0.01$).

Neonatal Weight

We controlled for the age of the infant at weighing by including it in the model as a covariate. The age of infant at weighing was statistically significant ($t_1=3.478$, partial $r^2=0.50$, $N=19$ infants, $P<0.005$).

Both E₁C and litter size were negatively and significantly related to neonatal weight (E₁C: $t_1=-2.212$, partial $r^2=0.29$, $N=17$, $P<0.05$; litter size: $t_1=-2.733$, partial $r^2=0.38$, $N=17$, $P=0.02$). Cortisol, on the other hand, was positively and significantly related to neonatal weight ($t=2.723$, partial $r^2=0.38$, $N=17$, $P=0.02$). The overall amount of variation in neonatal weight explained by the model (R^2) was 64%, and the model as a whole was significant (mixed-model ANOVA: $F_{4,12}=5.349$, $P=0.01$). Data are presented in Table 3.

Carrying (Week 1)

The average amount of observed time that mothers carried infants during week 1 was $72.7 \pm 6\%$ ($N=25$ infants). No factors in the model significantly predicted whether a mother would carry more than 50% of the time, or less than 50%.

Carrying (Weeks 2 and 3)

Mothers carried infants $39.6 \pm 3.5\%$ of observation time in weeks 2 and 3 ($N=32$ infants). Several factors were

significant in predicting maternal carrying effort in weeks 2 and 3. Mothers in larger groups carried their infants less (mixed-model ANOVA: $F_{1,13}=11.47$, $P<0.01$). Mothers carried singletons less than twins ($F_{1,13}=9.42$, $P<0.01$) and mothers at higher body weights carried more than mothers at lower body weights ($F_{1,13}=7.17$, $P=0.02$). An interaction existed between litter size and maternal weight (Fig. 1). The mother at a lower weight carried her singleton more than mothers at higher weights carried their singletons ($F_{1,13}=9.08$, $P=0.01$). This interaction was driven primarily by one data point (see Discussion).

Table 3. Raw data on infant neonatal weights, the age at which infants were weighed, and the rises in oestrogen conjugates and cortisol from baseline to the third trimester (ng/g faeces)

Infant	Weight (g)	Age (days)	Oestrogen conjugates (ng/g)	Cortisol (ng/g)
724	65	1	2317.08	1532.83
725	64	1	2317.08	1532.83
726	57	2	3406.73	332.71
727	55	2	3406.73	332.71
729	59	3	2536.04	888.33
730	67	3	2536.04	888.33
767	61	1	2243.26	967.94
436X3	67	2	4533.27	534.88
603X1	56	1	2243.26	967.94
651X1	69	8	946.41	-20.08
651X2	65	8	946.41	-20.08
AS2	67	4	3070.85	726.14
AS3	64	4	3070.85	726.14
AS4	53	1	8008.12	1423.91
AS5	61	1	8008.12	1423.91
ST21	63	2	1206.91	199.02
ST22	57	2	1206.91	199.02
ST23	54	2	N/A	N/A
ST24	60	2	N/A	N/A

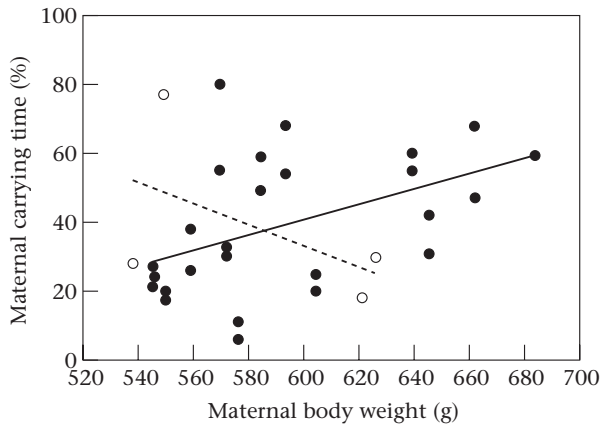


Figure 1. Maternal carrying time, expressed as a percentage of the total time observed during weeks 2 and 3 postpartum, by litter size (—●—: twins; --○--: singletons) and maternal body weight. $N=32$ infants.

Time on Nipple (Week 1)

On the average, infants spent $26.1 \pm 3.1\%$ of observation time on the nipple in week 1 ($N=25$ infants). No factors significantly predicted the amount of time infants spent nursing during week 1. There was a tendency for male infants to be on the nipple more than females (mixed-model ANOVA: $F_{1,8}=4.67$, $P=0.06$). Male infants spent $30.6 \pm 3.6\%$ of observation time on the nipple and females spent $16.4 \pm 4.5\%$.

Time on Nipple (Weeks 2 and 3)

The mean percentage of the total observation time that infants spent on the nipple in weeks 2 and 3 was $16.7 \pm 1.8\%$ ($N=32$ infants). Time on nipple during weeks 2 and 3 was predicted both by provisioning (infants of provisioned mothers nursed more; mixed-model ANOVA: $F_{1,14}=9.38$, $P<0.01$), and by group size (infants in smaller groups nursed more; $F_{1,14}=18.47$, $P<0.0001$; Fig. 2).

In an expanded model, which included one marginally significant fixed effect, time on nipple was predicted by provisioning (mixed-model ANOVA: $F_{1,13}=7.37$, $P=0.02$); group size ($F_{1,13}=20.42$, $P<0.001$); maternal weight (infants of mothers at higher weights nursed more; $F_{1,13}=4.15$, $P=0.06$); litter size (twins nursed more; $F_{1,13}=5.17$, $P=0.04$); and an interaction between maternal weight and litter size (the one mother of a singleton at a lower weight nursed her infant more; $F_{1,13}=5.07$, $P=0.04$).

DISCUSSION

The factors affecting early maternal care in golden lion tamarins are complex, and some appear to be more important than others. Hormonal factors are significantly involved in prenatal care as measured by neonatal weight, but not in the level of postnatal care. There is little evidence that sex of the infant affects maternal

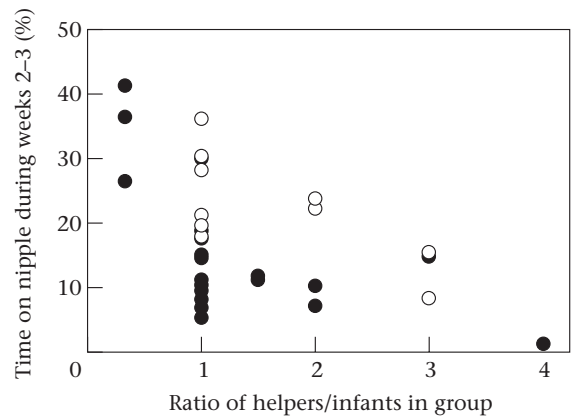


Figure 2. Time on nipple, expressed as a percentage of the total time observed during weeks 2 and 3 postpartum, by group size (number of group members, besides mother, per infants in group) and provisioning status of mother (●: nonprovisioned; ○: provisioned). $N=32$ infants.

care. We found no evidence of interactions between the sex of the infant and the condition of the mother. The primary factors that do affect postnatal maternal care in golden lion tamarins appear to be group size, maternal body weight, litter size and provisioning of the mother.

Why do some callitrichid mothers invest more than the minimum time and energy in caring for their young? Apparently, for two reasons: either because they have to or because they can. We found that the amount of help available to females was a strong predictor of both time on nipple and carrying time, as were maternal condition and litter size. Data from experimental tests (unpublished data), in combination with the fact that females do not generally lose weight during lactation (Dietz et al. 1994), have led us to believe that most females are not energetically stressed during the early infant care period. However, females at higher body weights, for any given group size, invest more in their young than those at lower body weights.

In contrast with results from recent studies on captive callitrichid primates (Pryce et al. 1988; Fite & French 2000) the present study did not find direct evidence for hormonal effects on maternal care in wild golden lion tamarins. There are several potential reasons for this. Faecal hormone levels are more variable than urinary or plasma concentrations, and we pooled values over a longer period than was used in previous studies done in captivity. It is possible that we failed to detect subtle variations in steroid concentrations that modify maternal motivation or performance. Furthermore, studies on captive marmoset and tamarin mothers contrasted hormonal profiles of females that successfully reared infants with those that did not. In the present study, early mortality of infants was very rare. Out of 40 infants alive at the onset of the study, three died during the first week and two more in the second week. Two of these deaths were from a triplet litter and may have been related to low neonatal weight, one was due to the predation death of the mother, and the final two were deaths to mothers that

previously and subsequently raised many infants to maturity. In other words, there appeared to be little or no mortality due to inadequate mothering. Finally, many of the effects that Pryce found (Pryce et al. 1988, 1995; Pryce 1993, 1996) can be related to interactions between hormone levels and parity (first-time mothers with low oestrogen showed poor maternal care, but not multiparous mothers with low oestrogen). We observed a large range of variation in maternal carrying in females with low oestrogen levels; however, our sample size of primiparous females was not sufficient to allow statistical analysis of the interaction between parity and oestrogen levels.

One area in which hormone levels were linked to prenatal maternal care was infant neonatal weight. Infants born to mothers with higher rises in E_1C weighed less, and those born to mothers with higher rises in cortisol weighed more. In humans, higher cortisol is associated with higher maternal insulin resistance, delayed metabolic clearance of glucose, and therefore more glucose available for the infant (Jovanovic-Peterson & Peterson 1996), which may explain the relationship we observed between cortisol levels and higher infant neonatal weight. Supporting evidence for this argument is that the female from this study that had the second highest increase in cortisol was the only female that gave birth to triplets. One intriguing possibility is that the cortisol rise in mothers with large infants may be triggered by the fetus rather than the mother (Haig 1993), perhaps via fetal corticotropin releasing factor. The relationship between neonatal weight and oestrogen conjugates may also be due to metabolic processes. In adult rats, higher oestrogen is associated with increased activity and decreased food intake (review in Wade & Schneider 1992). Oestrogens in callitrichids may exert their effects via a noninsulin dependent pathway, as they do in rats (Dudley et al. 1979). Although it is therefore possible that effects of cortisol and oestrogen are independent, measurement of hormone levels in faeces does not easily discern cause and effect sequences.

Also in contrast with other studies of maternal care in primates, we failed to find an overall effect of parity. Our sample included four primiparous females, with a mean carrying rate of $71.7 \pm 17\%$ in week 1, which is perhaps when one might expect the most differences in behaviour between experienced and inexperienced females. However, this result is only slightly different from the rate displayed by multiparous females ($73.1 \pm 6.5\%$). One salient fact is that all females in our study had infant care experience within their natal groups, which may have ameliorated the effects of being a first-time mother (review in Snowdon 1996).

In general, mothers at higher weights carried their infants more. However, the one mother at a lower weight that carried her singleton for a large percentage of time was also the only subordinate mother in our study. Data from this female were responsible for significance of the statistical interaction between litter size and weight of the mother, which may or may not reflect a true biological interaction. In wild common marmosets, subordinate mothers tend to be more protective of

their infants and carry them more (Digby 1994). The subordinate social status of the female in our study may be a better explanation of her high levels of maternal care than an interaction between her condition and litter size.

Nursing time has been criticized as an inaccurate measure of milk intake of the infant (review in Cameron 1998). In a species like golden lion tamarins, where mothers have control over the extent to which they carry an infant, variance in nursing time may be explained by two factors: time spent on the mother, and infant motivation to nurse. Infants in larger groups are on the nipple less in weeks 2 and 3, probably due to the fact that the mother carries less in large groups. Finally, infants of provisioned mothers are on the nipple more than infants of nonprovisioned mothers. While this result may be due to a difference in maternal condition, it is also possible that this is due to the fact that provisioned mothers spend less time foraging and more time sitting still (Stoinski 2000), thus allowing the infants to nurse more.

Finally, how do these results advance our understanding of the biological basis of cooperative breeding? Many studies of cooperatively breeding mammals and birds have concentrated primarily on the effects of group size on levels of parental care. As group size increases, parents may show either additive responses to increased numbers of helpers (i.e. per capita parental care does not decrease) or compensatory responses (i.e. per capita parental care decreases with more helpers) (Emlen 1997; Moehlman & Hofer 1997; Hatchwell 1999). In birds, either parent can feed the offspring, and the level of feeding may often limit offspring survival (Hatchwell 1999). When nestling starvation is infrequent, only females show a significant compensatory reduction in care (Hatchwell 1999). Most long-term studies on callitrichids show the opposite pattern. The number of helpers does not affect levels of maternal care, whereas the father shows a compensatory reduction in care in the presence of multiple helpers (review in Bales et al. 2000).

In the present study, however, we noted a compensatory effect of number of helpers on maternal carrying and nursing. One possible explanation for the differences we observed is that we examined offspring care over a shorter time frame than other studies. Our selection of the first 3 weeks corresponds to the time of greatest infant dependence on the mother. It may seem counterintuitive for a mammalian mother to reduce care in response to helpers during this period; after all, she is the only source of nutrition for her infants. However, female callitrichids also experience their first postpartum oestrus during this period (Wilson 1977). We now know that wild golden lion tamarin females at higher body weights give birth to larger litters (Bales et al. 2001). Compensatory reduction of maternal care during this period may therefore be a strategy leading to a larger subsequent litter, increased reproductive success for the female and higher inclusive fitness for the helper. A comparative study of helper effects on cooperatively breeding mammals with and without postpartum oestruses would be valuable in addressing this hypothesis.

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