Laboratory Animal Science
Vol 48, No 3
June 1998

Growth Variation in Common Marmoset Monkeys (*Callithrix jacchus*) Fed a Purified Diet: Relation to Care-Giving and Weaning Behaviors

Suzette Tardif,[1*] Cashell Jaquish,[2] Donna Layne,[1] Karen Bales,[3] Michael Power,[4] Rachel Power,[1] and Olav Oftedal[4]

Abstract | Significant relations were observed between select infant-care and weaning behaviors and growth in body weight in common marmoset monkeys (*Callithrix jacchus*). The patterns of these relations suggest that earlier occurrence of developmental milestones, such as cessation of transport (being off carriers) and weaning to solid food, were associated with slower growth during the subsequent period. In contrast, more frequent nursing bouts during the period in which weaning was initiated were associated with higher growth rates. In the case of being off carriers, these effects did not carry over to older ages, suggesting that any deficits in growth were temporary. In the case of earlier, more frequent consumption of solid food, there was some suggestion that there were longer-term effects, followed by catch-up growth. The knee-to-heel length of subjects was not related to the measured behaviors. There was no relation between early weaning to solid food and leanness at day 75, suggesting that, although this behavior was affecting overall weight, it did not affect relative gains of fat versus lean mass. There were, however, significant correlations between cessation of transport or frequency of nursing bouts during the weaning period and leanness, with earlier cessation of transport and less frequent nursing associated with leaner infants, after weaning. Our results differed from those of a previous study that found a relation between linear growth and abuse in this species, with abuse defined as physical injury by other members of the group. We found no differences in growth between abused and nonabused infants. However, abused infants had lower birth weight.

The common marmoset monkey (*Callithrix jacchus*) is a species of importance to biomedical research in fields as varied as infectious disease research, immunology, neuroscience, and reproduction. Part of the value of marmosets in research relates to their small body size, short generation time, and high fecundity. Although maximal fecundity in marmosets is the highest of all anthropoid primates, achieved levels of production are highly variable among colonies and among females within colonies (1–7). Such variation is seen even in colonies that have successfully addressed most of the nutritional and infectious disease concerns that plagued early efforts to breed marmosets. A better understanding of pre- and postnatal determinants of successful propagation in this species is required for its potential to be reached.

Measures of growth, such as changes in body weight, body length, or body composition, are frequently used as part of the assessment of efficacy of a captive propagation program. For example, age-specific weight has been found to be related to survivorship in common marmosets (8). Many factors can influence growth, such as genetics, nutrition, disease, and psychological stress or social deprivation, and much is known regarding the effects of extreme deficits in these factors on growth (9–11). However, for marmosets, little is known regarding the relationships between normal variation in psychosocial factors, nutrition, and growth processes.

The study reported here was designed to examine the relation between infant care and weaning behaviors and growth in a population of captive common marmosets. Johnson et al. (12) found that the quality of parental care in this species influenced later growth. Because the growth deficits they observed were associated with potential psychosocial stressors (i.e., abuse and neglect) and differences in hypothalamic-pituitary-adrenal function, they proposed that the common marmoset could provide a useful model for understanding psychosocial short stature and ensuing catch-up growth. However, they also pointed out that these deficits may be the results of nutritional differences among those infants receiving differing levels of care.

The difficulties inherent in differentiating the physiologic effects of psychosocial stressors from the differences in nutrition of infants receiving differing levels of care or subjected to different weaning patterns is a problem in studies of growth (11–13). For example, what might be classified as neglect in nonhuman primates may take the form of less frequent physical transport at early ages. This type of neglect, in addition to being a potentially potent psycho-

Department of Biological Sciences, Kent State University, Cunningham Hall, Kent, Ohio[1]; National Heart Lung and Blood Institute, National Institutes of Health, Bethesda, Maryland[2]; Department of Zoology, University of Maryland, College Park, Maryland[3]; Nutrition Laboratory, Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C.[4]
*Address correspondence to Dr. Suzette D. Tardif, Department of Biological Sciences, Kent State University, P.O. Box 5190, Kent, OH 44242-0001.

social stressor (14), may also result in higher energy expenditure for the growing infant through increased need for thermogenesis and independent locomotion; such increased energy expenditure could impair growth. In addition, weaning from dependence on milk to independent feeding represents a period of risk for growth retardation in primates (15), particularly if presentation of solid foods begins at an early age or inappropriate weaning foods are used.

The process of weaning in primates involves two transitions: the transition from physical transport during early infancy to completely independent locomotion, and the transition from dependence on milk as a sole food source to complete feeding independence. There can be significant variation in the timing of both of these weaning processes within a population (13, 16, 17). Although it has been proposed that this variation may be related to infant growth or condition (13, 16), detailed information on growth associated with variation in care and weaning behaviors in primates is limited.

We examined the association of growth variation with variation in weaning behaviors in a population of common marmosets fed a purified diet. Because diet was a controlled factor in this study, we were able to more precisely examine the effects of cessation of transport and weaning from milk to independent feeding. In addition to determining whether the association observed by Johnson et al. (12) between neglect or abuse and growth was present in this population, we intended to clarify the role of nutritional factors in behavior-associated growth variation in this primate species.

Materials and Methods

Subjects and housing: The animals of this study were housed in facilities (University of Tennessee and Kent State University) that have animal care and use programs accredited by AAALAC, International. All research protocols were approved by the relevant institutional animal care and use committees. The subjects of this study were 30 common marmoset infants born between May 1994 and April 1997 to 10 breeding pairs. Of the 30 infants, 22 were from litters of twins in which both were reared to weaning, and eight were singletons that were the result of either singleton births (n = 5) or litters of two to three in which only one infant survived more than 3 days (n = 3). Infants were housed, along with their parents and up to four older siblings, in cages measuring 182 x 152 x 91 cm. Cages were constructed of vinyl-coated hardware cloth and equipped with wooden branches and lexan nest boxes. Subjects were maintained on a 12/12-h light/dark cycle and at temperature of 25 to 27°C. Each group was visually isolated from other groups. As part of a study of protein and energy effects on pre- and postnatal reproductive investment, all groups were fed one of two isocaloric (3.7 kcal of metabolizable energy/g of diet) purified diets that differed in protein content (15% versus 25% metabolizable energy as protein) but were identical in fat content (5% by weight) and vitamin and mineral concentrations (Table 1). Previous studies of protein requirements of callitrichid primates indicate that both protein levels were sufficient for routine maintenance of captive marmosets (18, 19). The diets were presented twice a day so that food was available ad libitum; they were the only food item the animals received, with the exception of occasional treats used to reinforce behaviors such as standing on a scale or entering a catchbox. Extensive observations of feeding behavior indicated that individuals ate throughout the daylight hours. Infants were removed from their groups on the first day after birth for weighing and measurement. Individuals in twin litters were distinguished by marking the coat of one with a peroxide bleach. Attempts were made to handle all infants in a similar fashion.

Table 1. Composition of purified diets

Ingredient	15% Protein diet	25% Protein diet
Lactalbumin	160 g/kg	275 g/kg
Dextrin	509 g/kg	397.2 g/kg
Sucrose	145 g/kg	145 g/kg
Soybean oil	40 g/kg	47 g/kg
Cellulose	50 g/kg	50 g/kg
Vitamin/mineral mix	82.8 g/kg	82.8 g/kg
Energy	3.7 kcal/g	3.7 kcal/g

Measures of growth. *Weight:* Infants were removed at least once a week for weighing up to approximately day 35 to 40. After this time, the infants could be weighed in their home cage by placing a scale in the cage. Weight was available through the age of 120 days for all 30 subjects and through 220 days for 28 subjects. Weight was measured on a digital scale to the nearest gram. Similar to other primate species, common marmosets exhibit rapid infant growth, with gradual slowing during late adolescence. The most rapid increase in body weight occurs prior to 100 days of age (12, 20, 21).

Body length: At day 75, knee-to-heel length was measured on all subjects, using a set of vernier calipers, to the nearest 0.01 cm.

Body composition: At day 75, total body water content was measured for 14 of the subjects, using a labeled-water dilution method (22). Given that body water is directly proportional to the fat-free mass of the body (23), the ratio between body water and body weight was used as an estimate of relative leanness (referred to hereafter as the leanness index). Therefore, a higher leanness index reflects a higher fat-free-to-fat ratio.

Behavioral measures: Infants in all groups were observed one to three times daily for the first 14 days of life and approximately 3 times per week from day 15 through day 70. Observation sessions were 30 min in duration and were spread throughout the day, from 0800 to 1700 h. During each observation session, the infants served as focal animals, and all occurrences of the following behaviors were scored:

Infant carried: infant clinging by at least two limbs and its weight supported (scored as a state—duration known);

Infant harassed: infant is grabbed, bitten, or rubbed on the side of the cage by the animal transporting it (scored as an event);

Infant nursed: infant is in the axial position, on the mother's nipple. Although it is difficult to distinguish nutritive from non-nutritive suckling in marmosets (24), it has been reported that non-nutritive suckling appears to be less common in New World primates than in Old World species (25). Therefore, this measure is assumed to be a reliable indicator of daytime suckling frequency (scored as a state–duration known).

Infant eats: infant ingests food (scored as a state—duration known). Comparison of measured food intake versus time spent eating for a separate set of subjects indicated that time spent eating was a good indicator of relative amount of food eaten by animals fed these purified diets. The correlation between percentage of time spent eating (measured in 14- or 15-min observations, spread throughout 2 days) and weight of food consumed during 48 h for five individual adult animals consuming this diet was 0.928.

Abuse measures: Infants were observed for signs of abuse when they were removed for weighing, as well as during behavioral observations. Abuse consisted of tail biting, resulting in the loss of at least a third of the length of the tail, and injuries to the hands and face. These observations were used, in manner fashion similar to that reported by Johnson et al. (12), to classify infants as abused versus nonabused.

The study period for each subject was divided into three periods on the basis of published information regarding the behavioral ontogeny of this species (24, 26, 27), with emphasis placed on behaviors related to acquisition of nutrients:

Days 0 to 21: Little or no independent feeding or locomotion is typical;

Days 22 to 42: A transitional period, at the end of which virtually all locomotion is independent and independent feeding has begun;

Days 43 to 70: A period during which all locomotion is independent, all animals are independently feeding, but nursing still occurs.

Using the behaviors and growth parameters measured, the following variables were calculated:

Percentage of time off carriers (days 0 to 21);

Percentage of time suckling and frequency of suckling bouts (days 22 to 42);

Percentage of time eating independently (days 22 to 42);

Frequency of harassment per observation period (days 0 to 21 and 22 to 42);

Age-specific weight at the end of the time period (days 0 to 21, 22 to 42, 43 to 70);

Growth rate, as grams gained per day throughout the period (days 0 to 21, 22 to 42, 43 to 70).

Analysis of data: Initially, the relation of behavioral parameters to growth parameters for the same and subsequent periods was determined by calculating bivariate correlations. Behavioral measures that were scored as a percentage were arcsin-square-root transformed prior to calculation of Pearson correlations. For other behaviors, Spearman correlations were used. In some instances, examination of correlations revealed an apparent relation between occurrence (versus lack of occurrence) of a behavior during a specific period and subsequent growth. In these instances, the relation between occurrence of weaning behaviors and growth was determined by use of *t* tests, with occurrence versus non-occurrence of behavior used to classify subjects.

To determine whether behaviors that were significantly correlated with early increase in weight were also related to the other measures of growth, correlations between these behaviors and knee-to-heel length and the leanness index (day 75) were calculated. To determine whether behaviors that were related to early growth had lasting effects, the correlations between these behaviors and later growth measures were examined. Specifically, the correlations between behaviors that affected early growth and day-120 to day-220 growth rate (in weight) were determined, as previously described.

The relation between abusive behaviors and growth was examined in two ways. Correlations between frequency of harassment and the growth parameters were determined by calculating Spearman correlation coefficients. Also, early and late growth parameters were compared in abused versus nonabused infants, as previously defined, by use of *t* tests.

All statistical analyses were conducted using SPSS software.

Results

Overall growth in body weight from birth to day 120 (1.11 g/day) was similar to that reported for other captive colonies of this species (1.0 to 1.4; [28]). The potential impact of three factors other than the behaviors of interest on growth were first determined. Group size was not related to any growth parameter. Litter size was related to the leanness index, with twins being leaner than singletons. However, behavioral effects on leanness were the same across litter sizes. The seven subjects fed the higher-protein diet (25%) differed from the 23 subjects fed the lower-protein diet (15%) in one growth parameter: the higher-protein group had lower mean weight (68.2 + 15.9 g versus 81.3 + 12.4 g; *t* test = 2.28, $P = 0.031$) at day 42, compared with the lower-protein group. However, behavioral effects on growth were the same across diets. Because the behavioral effects that were observed were the same across litter sizes and protein concentrations, it was considered appropriate to pool subjects across these conditions for further analyses.

Association between behaviors and early growth in weight: Three behaviors were associated with early growth in weight (Table 1).

Days 0 to 21: The percentage of time that infants were off carriers during the earliest period (days 0 to 21) was negatively associated with growth and age-specific weight during the next period (days 22 to 42). That is, infants that were off transport more often during the first 3 weeks grew more poorly during the subsequent 3 weeks and had lower day-42 weights than did infants that were carried more often. Percentage of time off carriers during days 0 to 21 tended to be negatively associated with birth weight (Pearson correlation = -0.318, $P = 0.086$). A partial correlation of percentage of time off carriers to growth, controlling for birth weight, was still significant (correlation with

Table 2. Relation between select behaviors and early growth in common marmosets

Variable	Day-21 weight	Growth rate days 0–21	Day-42 weight	Growth rate days 22–42	Day-70 weight	Growth rate days 43–70
% Off transport	-0.289	-0.194	**-0.423**	**-0.464**		
Days 0–21	*P* = 0.121	*P* = 0.304	***P* = 0.020**	***P* = 0.010**		
Frequency of suckling			0.157	**0.406**	0.320	0.244
Days 22–42			*P* = 0.450	***P* = 0.044**	*P* = 0.119	*P* = 0.240
% Eating			-0.185	-0.049	**-0.400**	**-0.436**
Days 22–42			*P* = 0.347	*P* = 0.805	***P* = 0.035**	***P* = 0.020**

growth rate, days 22 to 42 = -0.377, *P* = 0.022; with day-42 weight = -0.304, *P* = 0.055).

Days 22 to 42: Two behaviors measured during this period were associated with growth; neither behavior was associated with birth weight. The frequency of suckling bouts per observation period during days 22 to 42 was positively correlated with growth rate during the same period (Table 2). The percentage of time that infants spent eating solid food during days 22 to 42 was negatively associated with growth and age-specific weight during the next period (days 43 to 70). The mean growth rate for infants that ate <1% of the time versus those spending more than 1% of the time eating was significantly different (*t* test for means with unequal variance; *t* = 2.14, *P* = 0.049; Figure 1A).

Once the association between these behaviors and early growth was established, we determined whether these behaviors were related. There was no association between frequency of suckling bouts and time off carriers or time spent feeding. However, percentage of time off carriers (days 0 to 21) and percentage of time feeding (days 22 to 42) were negatively correlated (correlation coefficient = -0.386, *P* < 0.04).

Association between early behavior and other growth parameters: There was no relation between any of the behavioral parameters and day-75 knee-to-heel length. There was also not a significant correlation between percentage of time feeding and leanness index; however, this variable was related to early time off carriers and to suckling frequency. There was a negative correlation between suckling bout frequency during days 22 to 42 and leanness index (day 75; correlation = -0.800, *P* = 0.003); infants that suckled less frequently during days 22 to 42 were leaner than infants suckling more frequently; this relation was linear (Figure 2). There also was a significant positive correlation between percentage of time off carriers during days 0 to 21 and leanness index (correlation = 0.699, *P* = 0.003); infants that were off carriers more during days 0 to 21 were leaner at day 75.

Relation of behaviors to later growth: The percentage of time off carriers (days 0 to 21) was not related to later growth (days 120 to 220). There was a trend, however, for percentage of time spent eating solid food during days 22 to 42 to be related to later growth in a manner suggestive of catch-up growth. Specifically, there tended to be a negative relation between percentage of time eating solid food (days 22 to 42) and day-120 weight (i.e, animals that fed more frequently at an earlier age had lower day-120 weight; Pearson correlation = -0.339, *P* = 0.077), but a positive association between such feeding time and growth rate from 120 to 220 days (i.e., animals that ate solid food more frequently at an earlier age had higher later growth rates; Pearson correlation = 0.334, *P* = 0.08). The later

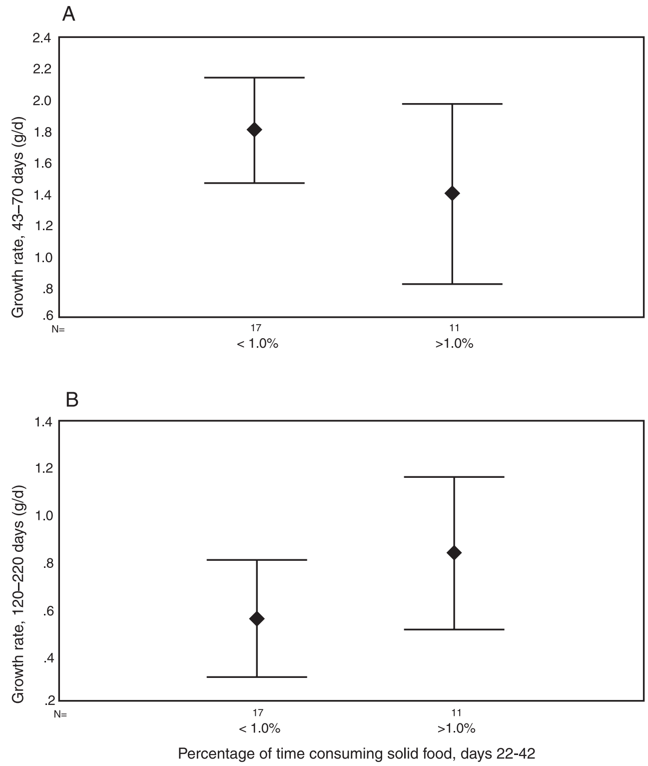

Figure 1. Growth rate (mean ± SD) from **(A)** days 43 to 70 and **(B)** days 120 to 220 for infants that ate solid food <1% of observation time during early weaning (days 22 to 42) versus those eating more than 1% of observation time.

growth rate for infants that ate more during the weaning period was significantly higher than the rate for infants that ate <1% of the time during the weaning period (*t* test: *t* = -2.50, *P* = 0.019; Figure 1B).

Relation of harassment and abuse to growth: There was no relation between the frequency of harassment and any growth parameter. Table 3 provides weight and growth comparisons for abused versus nonabused infants. Abused and nonabused infants did not differ in any postnatal growth parameters; they did, however, differ in birth weight. Abused infants had significantly lower birth weight than did nonabused infants (*t* test value = 2.10, *P* = 0.045).

Discussion

Our finding of an association between the amount of time infants are carried during the earliest period and growth was similar to the findings of Johnson et al. (12) for a different captive population of common marmosets. These findings, as well as those of Jaquish (21), suggest that earlier, more frequent independent locomotion in this primate

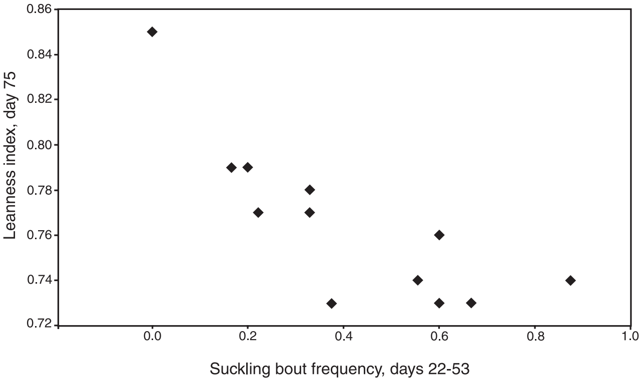

Figure 2. Frequency of suckling bouts per observation period during days 22 to 42 versus leanness index, measured at day 75. The leanness index is total body water per body weight, with total body water determined through radiolabeled-water dilution.

may be a stressor that affects subsequent growth. This stressor might be psychosocial or nutritional, or both. Although the relation observed by Johnson et al. (12) lasted into the juvenile period (day 140), the effect seen in our population appeared to be transitory. There was a marked difference in age-specific weight between the two populations being studied: the infants of this study were, on average, 25 to 33% heavier at days 75 and 120. It is possible that more severe behavioral or nutritional stressors were present in the population that had more long-lasting effects on growth.

The association of growth with behaviors related to weaning from milk to solid food suggests that nutritional factors were important determinants of early weight gain in this marmoset population. Specifically, behavior associated with more frequent access to milk (i.e., frequency of suckling bouts) during the initiation of weaning correlated with better growth and less lean infants, whereas more frequent ingestion of solid food during this period was associated with poorer gain in overall weight. Infants that ate more solid food during early weaning did not necessarily suckle the least. However, we have documented significant variation in milk composition in this population (29), and preliminary data suggest that infants eating more solid food during early weaning were receiving milk that was lower in gross energy content (30). Future analyses should reveal the relative importance of each of these factors (milk quality, milk quantity, and rate of weaning to solid food) to growth.

Weaning processes are likely to involve a complex interaction of changes in the infant's and the mother's experience and physiology, as is the case in better-studied mammals such as the rat (9, 31, 32). The study reported here did not allow a decisive delineation of the role of the mother versus the infant in the generation of the variable growth and behavior patterns that were observed. However, some observations point to the likelihood that alterations in maternal behavior and physiology were a driving force behind the premature weaning that was associated with poorer growth. Marmosets have a communal infant care

Table 3. Comparison of abused and nonabused infants. Abuse was defined as physical injury to the infants by the parents or helpers.

Variable	Abused (n = 5)	Non-abused (n = 25)
Birth weight (g)*	27.4 + 3.21	30.6 + 3.29
Days 0–21 growth rate (g/d)	0.77 + 0.15	0.84 + 0.35
Days 22–42 growth rate	1.44 + 0.34	1.41 + 0.45
Day-120 weight	168.5 + 20.6	182.7 + 27.5

*Different by *t* test, $P < 0.05$; others are not significantly different
Data are expressed as mean ± SD

pattern in which infants are transported frequently by group members other than the mother. Mothers principally control infant access to suckling during early infancy through retrieving infants from other carriers or harassing carried infants until they are removed (26, 27). In this population, there was a positive correlation between frequency of suckling bouts and maternal body weight (30), suggesting that mothers in poorer condition may have nursed their infants less frequently. Studies of other primates also found a relation between maternal condition and maternal behavior (6, 7).

Earlier weaning to solid foods was behaviorally separate from early cessation of transport. There was some suggestion that the effects of earlier weaning to solids may have been longer lasting than those effects associated with earlier cessation of transport. The trend toward a lower day-120 weight being associated with earlier, more frequent ingestion of solid food could be important in that, when examining a larger population, we previously found an association between day-120 weight and survival in this species (8). However, in the present population there was evidence of catch-up growth occurring after day 120, as the growth rate of the group that fed more frequently during the weaning period was significantly higher from days 120 to 220.

There was some suggestion that the effects of early weaning from carrying were more closely related to birth condition than were the effects of early weaning to solid food. The other significant behavioral outcome during the earliest period (physical injury to the infants by parents or helpers) also was associated with lower birth weight. Our results are in contrast to those of another study (12), in that we did not find a relation between any growth parameter and abuse (as defined by physical injury) in our population. Because birth weights of the infants in the previous study were not available, it is not possible to tell whether disparity in weight and perhaps, therefore, in maturity or general condition at birth may have been a factor in the relation between abuse and growth. Observations of parturition make it clear that a certain level of maturity and vigor on the part of the infant is necessary for survival in this species (24, 33). In addition, results of numerous studies of rodents make it clear that the interactions of mothers and infants are dependent on the relative stage of lactation of the mother and the relative maturity of the infant (9). Therefore, abuse might be more likely in small or premature infants that are too weak to display normal clinging behavior or that display other abnormalities in response to the mother. This relation seems likely, given that behaviors that are classified as abuse in this species are often extreme variants of the behaviors normally displayed to dislodge an infant that is being normally carried.

In conclusion, behaviors indicative of early cessation of transport as well as early weaning from milk to solid food were related to transitory deficits in weight gain in this common marmoset population. Behaviors classified as abuse were not associated with growth deficits, as has been reported in other populations of this species, but were associated with lower birth weight and, therefore, perhaps with relative immaturity at birth.

Acknowledgements

This research was supported by NIH grant no. R01-RR02022.

References

1. **Hearn, J. P., S. F. Lunn, F. J. Burden, *et al.*** 1975. Management of marmosets for biomedical research. Lab. Animals **9:**125–134.
2. **Poole, T. B., and R. G. Evans.** 1982. Reproduction, infant survival and productivity of a colony of common marmosets (*Callithrix jacchus jacchus*). Lab. Animals **16:**88–97.
3. **Hiddleston, W. A.** 1978. The production of the common marmoset *Callithrix jacchus*, p. 51–57. *In* D. J. Chivers and W. Lane Peter (ed.), Recent advances in primatology. Academic Press, Inc., New York.
4. **Tardif, S. D., C. B. Richter, and R. L. Carson.** 1984. Reproductive performance of three species of Callitrichidae. Lab. Anim. Sci. **34:**272–275.
5. **Heger, W., and D. Neubert.** 1988. Maintenance and breeding of *Callithrix jacchus* in a colony in Berlin, p. 53–70. *In* Non-human primates: developmental biology and toxicology. Ueberreuter Wissenschaft, Berlin.
6. **Koenig, A., U. Radespiel, M. Siess, *et al.*** 1990. Analysis of pairing-parturition intervals and interbirth intervals in a colony of common marmosets. Z. Saugetierk. **55:**308–314.
7. **Jaquish, C. E., T. B. Gage, and S. D. Tardif.** 1991. Reproductive factors affecting survivorship in captive Callitrichidae. Am. J. Phys. Anthropol. **84:**291–305.
8. **Jaquish, C. E., S. D. Tardif, and J. M. Cheverud.** 1997. Interactions between infant growth and survival: evidence for selection on age specific body weight in captive common marmosets (*Callithrix jacchus*). Am. J. Primatol. **42:**269-280.
9. **Hennessey, M. B., N. K. Laughlin, S. G. Weiner, *et al.*** 1980. Malnutrition and maternal behavior in the rat, p. 211–234. *In* R. W. Bell and W. P. Smotherman (ed.), Maternal influences and early behavior. Spectrum Press, Jamaica, New York.
10. **Allen, L. H.** 1994. Nutritional influences on linear growth: a general review. Eur. J. Clin. Nutr. **48:**S75–S89.
11. **Skuse, D., S. Reilly, and D. Wolke.** 1994. Psychosocial adversity and growth during infancy. Eur. J. Clin. Nutr. **48:**S113–S130.
12. **Johnson, E. O., T. C. Kamilaris, A. E. Calogero, *et al.*** 1996. Effects of early parenting on growth and development in a small primate. Pediatr. Res. **39:**999–1005.
13. **Altmann, J., and A. Samuels.** 1992. Costs of maternal care: infant-carrying in baboons. Behav. Ecol. Sociobiol. **29:**391–398.
14. **Coe, C. L.** 1990. Psychobiology of maternal behavior in nonhuman primates, p. 157–183. *In* N. A. Krasnegor and R. S. Bridges (ed.), Mammalian parenting. Oxford University Press, Oxford.
15. **Altmann, J.** 1980. Baboon mothers and infants. Harvard University Press, Cambridge.
16. **Lee, P.** 1987. Nutrition, fertility and maternal investment in primates. J. Zool. (London) **213:**409–422.
17. **Fairbanks, L. A., and M. T. McGuire.** 1995. Maternal condition and the quality of maternal care in vervet monkeys. Behaviour **132:**733–754.
18. **Flurer, C., and H. Zucker.** 1985. Long-term experiments with low dietary protein levels in Callitrichidae. Primates **26:**479–490.
19. **Barnard, D., and J. J. Knapka.** 1995. Callitrichid nutrition, p. 55–82. *In* N. K. Clapp (ed.), A primate model for the study of colitis and colonic carcinoma: the cotton-top tamarin. CRC Press, Boca Raton, Fla.
20. **Abbott, D. H., and J. P. Hearn.** 1978. Physical, hormonal and behavioral aspects of sexual development in the marmoset monkey, *Callithrix jacchus*. J. Reprod. Fertil. **53:**155–166.
21. **Jaquish, C. E.** 1993. Genetic, behavioral and social effects on fitness components in marmosets and tamarins (family: Callitrichidae). Ph.D. dissertation, Washington University, St. Louis, Mo.
22. **Power, R. A., M. L. Power, D. G. Layne, *et al.*** 1996. Relations between measures of body composition in the common marmoset. XVIth Congress, International Primatology Society, #352.
23. **Schoeller, D. A.** 1996. Hydrometry, p. 25–43. *In* A. F. Roche, S. B. Heymsfield, and T. G. Lohman (ed.), Human body composition. Human Kinetics, Champaign, Ill.
24. **Missler, M., J. R. Wolff, H. Rothe, *et al.*** 1992. Developmental biology of the common marmoset: proposal for a “postnatal staging.” J. Med. Primatol. **21:**285–298.
25. **Rosenblum, L.** 1968. Mother-infant relations and early behavioral development in the squirrel monkey, p. 207–234. *In* L. A. Rosenblum and R. W. Cooper (ed.), The squirrel monkey. Academic Press, Inc., New York.
26. **Ingram, J. C.** 1977. Interactions between parents and infants and the development of independence in the common marmoset (*Callithrix jacchus*). Anim. Behav. **25:**811–827.
27. **Yamamoto, M. E.** 1993. From dependence to sexual maturity: the behavioral ontogeny of Callitrichidae, p. 235–256. *In* A. B. Rylands (ed.), Marmosets and tamarins: systematics, behavior and ecology. Oxford University Press, Oxford.
28. **Kirkwood, J. K.** 1985. Patterns of growth in primates. J. Zool. (London) **205:**123–136.
29. **Power, M. L., O. T. Oftedal, and S. D. Tardif.** Does the composition of milk of a callitrichid monkey reflect their small body size? Submitted for publication.
30. **Tardif, S. D., M. L. Power, and O. T. Oftedal.** Unpublished results.
31. **Dollinger, M. J., W. R. Holloway, and V. H. Dennenberg.** 1980. The development of behavioral competence in the rat, p. 27–56. *In* R. W. Bell and W. P. Smotherman (ed.), Maternal influences and early behavior. Spectrum Press, Jamaica, New York.
32. **Alberts, J. R.** 1994. Learning as an adaptation of the infant. Acta Paediatr. Suppl. **397:**77–85.
33. **Rothe, H.** 1974. Further observations on the delivery behavior of the common marmoset (*Callithrix jacchus*). Z. Saugetierk. **39:**135–142.