

Nighttime Wakefulness Associated with Infant Rearing in *Callithrix kuhlii*

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*Parent-infant cosleeping occurs in human and nonhuman primates, yet studies on the impact of cosleeping on parental sleep patterns have been limited to human mothers. We examined the effects of cosleeping on the nighttime wakefulness of a biparental New World primate, Wied's black tufted-ear marmoset (*Callithrix kuhlii*). We compared the sleep patterns of marmoset parents caring for young infants to those without infants, using an 8 mm videocamera and timelapse VCR under infrared illumination. The presence of young infants significantly impacted the sleep of mothers but not fathers. In fact, mothers rearing young infants were awake >3 times as often as mothers without infants. We also examined the nighttime wakefulness of marmoset parents across the first 9 weeks of infant life (birth through weaning). Although callitrichid mothers tend to reduce their daytime investment in offspring very early in infant life by relinquishing the care of infants to fathers and alloparents, increased nighttime wakefulness was not limited to the early postpartum period for the mothers. Instead, mothers exhibited more nighttime wakefulness than fathers did across the first 9 weeks of infant life. Our results indicate that the presence of infants has a greater impact on the sleep patterns of *Callithrix kuhlii* mothers than fathers, suggesting that mothers are more involved in infant care than previously realized and that fathers are not nearly as involved in nighttime care as their behavior during the day would suggest.*

KEY WORDS: maternal behavior, infant care, sleep, co-sleeping, callitrichid.

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INTRODUCTION

While all female primates incur energetic costs associated with producing and caring for offspring, Callitrichidae face even greater energetic demands. Marmosets and tamarins typically produce large twin litters, which at birth can weigh as much as 15–25% of the female's body weight (Kleiman, 1977) and, unlike other primates, callitrichid females do not exhibit lactational suppression of ovulation (e.g., French, 1983; Lunn and McNeilly, 1982; but also see Ziegler *et al.*, 1990). Instead, a postpartum estrus occurs 2–4 weeks following birth (e.g., French *et al.*, 1996; Ziegler *et al.*, 1987), so that they can conceive and commence gestation while still carrying and nursing their current litter of highly dependent, large twin infants. Therefore, callitrichid reproduction appears to be particularly costly for mothers, especially when conception occurs during the early postpartum period.

These energetic demands have often been cited as factors necessitating some form of assistance for callitrichid mothers and, indeed, cooperative rearing of offspring is a hallmark of reproduction in marmosets and tamarins (e.g., Tardif *et al.*, 1993). In every species studied to date, fathers and alloparents, i.e., older offspring and, sometimes, unrelated individuals living in the social group, assist mothers in every form of infant care except nursing (e.g., Cleveland and Snowdon, 1984; Goldizen, 1987). In fact, investigations into the allocation of infant carrying effort, which is likely the most energetically costly form of infant care that mothers can relinquish to others, have revealed that mothers often spend less time carrying infants than fathers do (Snowdon, 1996). Some mothers reduce their carrying effort even further as their families grow and alloparental assistance becomes available (e.g., Bales *et al.*, 2002; Cleveland and Snowdon, 1984; Santos *et al.*, 1997; Tardif *et al.*, 1990). Thus, the emerging picture of maternal investment in marmosets and tamarins, when one considers general patterns of daytime infant care, is one of little postnatal maternal investment in infants, beyond nursing, relative to the high levels of paternal and alloparental investment.

An additional potential cost for callitrichid mothers rearing infants that has not yet been assessed is related to the close physical contact maintained between infants and their caregivers during the night. Cosleeping, which has been defined as an infant sleeping in contact with another individual, or at least close enough to receive, react to, or exchange sensory stimuli, is routinely practiced among humans by the majority of the world's nonindustrialized cultures and is common in American society (e.g., Mosko *et al.*, 1997b). Like many human families, marmoset and tamarin group members sleep in close proximity to one another and to their infants; callitrichid primates sleep huddled together in tree holes, tangles of vines, and on dense pads of vegetation (Sussman and Kinzey, 1984), with young infants clinging to the

back of a parent (Hershkovitz, 1977). While huddling and sleeping in close contact with family members may serve beneficial antipredator (Coimbra-Filho, 1977) or thermoregulatory functions or both (Thompson *et al.*, 1994) for marmosets and tamarins, there may be other consequences associated with sleeping with infants. For instance, cosleeping human mothers and infants exhibit more arousals and more partner-induced arousals, exhibit more frequent shifts in sleep stages, and spend more time in the same sleep stage or awake while sleeping together in the same bed than when sleeping apart (e.g., McKenna *et al.*, 1993; Mosko *et al.*, 1997a). Accordingly, parent-infant cosleeping can have a significant impact on the sleep architecture of human mothers. Similarly, parent-infant cosleeping also could affect the sleep architecture of cosleeping nonhuman primates and might represent an additional cost of rearing infants.

We present the first study on the impact of parent-infant cosleeping on the sleep patterns and nighttime behavior of a callitrichid species. The purposes of the study were twofold. First, we wanted to determine whether less or disrupted sleep might be associated with rearing, and therefore sleeping with, infants. Therefore, we compared the nighttime wakefulness of adult marmosets with, and without, young infants in their family groups. Second, we examined the impact of infants on parental sleep patterns and nighttime activity levels from birth through weaning, in light of naturally occurring changes in the parent-infant relationship as infants mature and gain independence. We monitored patterns of nighttime wakefulness and nighttime activity in adult marmosets across the first 9 weeks of infant life (birth through weaning).

METHODS

Subjects

The subjects were Wied's black tufted-ear marmosets (*Callithrix kuhlii*) housed at the University of Nebraska at Omaha's Callitrichid Research Center. They live in large cages (1.6 × 0.9 × 2.4 m) constructed of wooden frames and wire mesh walls, containing a removable transport cage, natural branches, a feeding platform, a nest box, and numerous enrichment devices. A 12 hr:12 hr light:dark cycle was controlled via automatic timers, with light onset occurring at 0800 hr.

To assess the impact of infants on the sleep and nighttime activity of marmoset parents, we recorded the nighttime behavior of 4 family groups without infants and 8 different family groups with infants. Family groups without infants contained no offspring <6 mo old. Family groups with infants

were rearing either a twin litter ($n = 7$) or a singleton ($n = 1$), and the infants were ≤ 14 d old. During this stage of infant development, infants are critically dependent on caregivers for warmth and nourishment, spending all of their time being carried by another family member (e.g., Missler *et al.*, 1992; Tardif *et al.*, 1993, 1998). We recorded the families in this portion of the study on 2 consecutive nights. Then we averaged the scores from the 2 nights to provide an estimate of nighttime behavior when adults were, and were not, caring for offspring. To ensure intra-group similarity of the subjects, we conducted independent t tests on demographic and reproductive parameters. A great deal of similarity between marmoset family groups with and without infants was indicated; comparisons of the age of the mothers ($t = -0.60$, $df = 10$, n.s.), the age of the fathers ($t = -0.54$, $df = 10$, n.s.), the prior number of litters born to each breeding pair ($t = -0.72$, $df = 10$, n.s.), and the number of juveniles present within each family group ($t = -0.56$, $df = 10$, n.s.), revealed no significant differences among the family groups with and without infants.

To assess the impact of infants on parental sleep and nighttime behavior as infants mature and become less dependent on their caregivers, we conducted a separate series of observations on 5 family groups. Each family group contained newborn twin litters. For the first 9 weeks of infant life (birth through weaning), we videorecorded the nighttime behavior of each family group on 2 consecutive nights and averaged the scores from each week to provide a weekly estimate of nighttime behavior.

Assessment of Nighttime Wakefulness

We videotaped each family group during the dark phase of the 12:12-h light cycle on which they were maintained. We scored video footage via instantaneous sampling at 5-min intervals, with the breeding male and female of each group scored separately. We used a Sony 8 mm recorder (model # SR-L901U) and a Lilin black-and-white monitor (model # PIH-12) to record and to observe adult and infant sleep patterns, respectively. A 250-W GE infrared heat lamp-bulb positioned at the end of the cage opposite the nesting area provided illumination throughout the night. Positioning the lamp a minimum of 2.4 m (length of cage) from the nest area, we achieved the illumination of the nest box with minimal heat. We monitored the ambient temperature of each colony room on a 24-h basis and maintained a constant 25°C. Before collecting data, all groups had at 2-3 nights to habituate to the camera and lamp.

We assessed nighttime wakefulness by recording the number of sampling points at which animals were clearly awake while in their nests. To avoid ambiguity in scoring wakefulness, we scored only monkeys that were active, i.e., grooming, interacting with others or interacting with infants, or

sitting still with eyes wide open, while in their nests, as awake. We did not score individuals exhibiting myoclonus or slow eye movements as awake. We used the totals to calculate the percentage of sampling points, during the dark phase of their light cycle, at which each adult was awake. We determined general activity levels by recording the number of sampling points at which individuals were away from the nest during the dark phase of the light cycle. To better understand when differences in wakefulness and nighttime activity might occur, we collapsed the intervals from the 12-h lights out phase into three 4-h periods, late evening (2000 – 2359 h), early morning (2400 – 0359 h), and late morning (0400 – 0759 h).

Before scoring all videotapes at 5-min intervals, we scored five 12-h videotapes at 1-min intervals and at 5-min intervals. We used Pearson correlation coefficients to assess the validity of scoring videotapes at 5-min intervals. Measures of wakefulness from videotapes scored at 1-min and 5-min intervals are positively and significantly correlated ($r = 0.98$, $p < 0.001$). Interobserver reliability measures, for the 4 individuals (Fite, Hopkins, Patera, Rukstalis) who scored tapes, were above 92%.

Analyses

To compare wakefulness and nighttime activity in adult marmosets with and without newborn infants in their family groups, we conducted 3-way mixed ANOVA's (sex x infant presence/absence x time period) on nighttime wakefulness and time away from the nest. To examine the impact of infants on parental wakefulness and time away from the nest, from birth through weaning, we conducted 3-way mixed ANOVA's (sex x infant age x time period) on nighttime wakefulness and time away from the nest. We conducted analyses post hoc via the Tukey test (Keppel, 1991). We adopted an α level of 0.05 for all statistical tests.

RESULTS

Impact of Infants on Nighttime Wakefulness and Time Out of the Nest

Adult marmosets exhibited distinct patterns of nighttime wakefulness (Figure 1A). Regardless of the presence of infants, parents were significantly more likely to be awake while in their nests during late evening hours (2000 – 2359 h) than during early (2400 – 0359 h) or late morning hours (0400 – 0759 h; $F(2, 40) = 48.54$, $p < 0.001$).

Caring for young infants was associated with increased nighttime wakefulness in marmoset mothers (Figure 1B). A significant interaction between

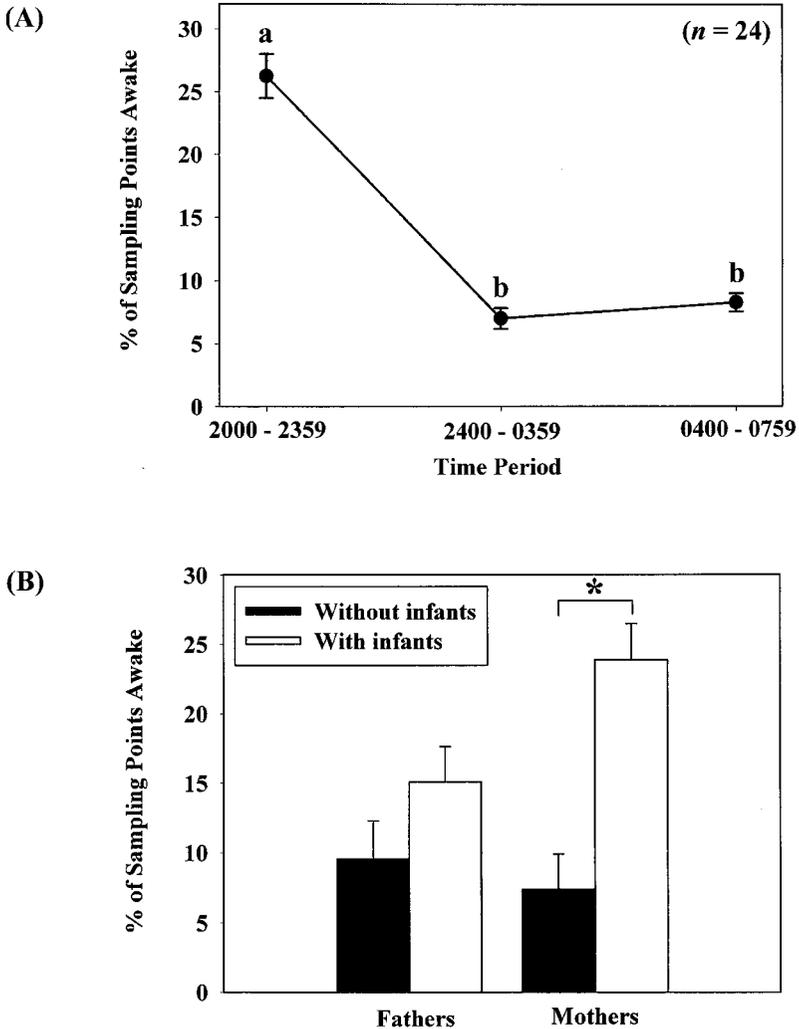


Fig. 1. (A) Mean percentage of sampling points (\pm SEM) that adult marmosets were awake during late evening, early morning, and late morning hours. Time periods demarked by different letters differ significantly from one another, $p < 0.05$. (B) Mean percentage of sampling points (\pm SEM) that adult marmosets, with and without infants, were awake during the night. * $p < 0.05$

sex and infant presence/absence ($F(1, 20) = 4.64$, $p < 0.05$) indicated that the relationship between infant presence and wakefulness was dependent on the sex of the parent. Analyses post hoc revealed that mothers, but not fathers, were significantly more likely to exhibit nighttime wakefulness when

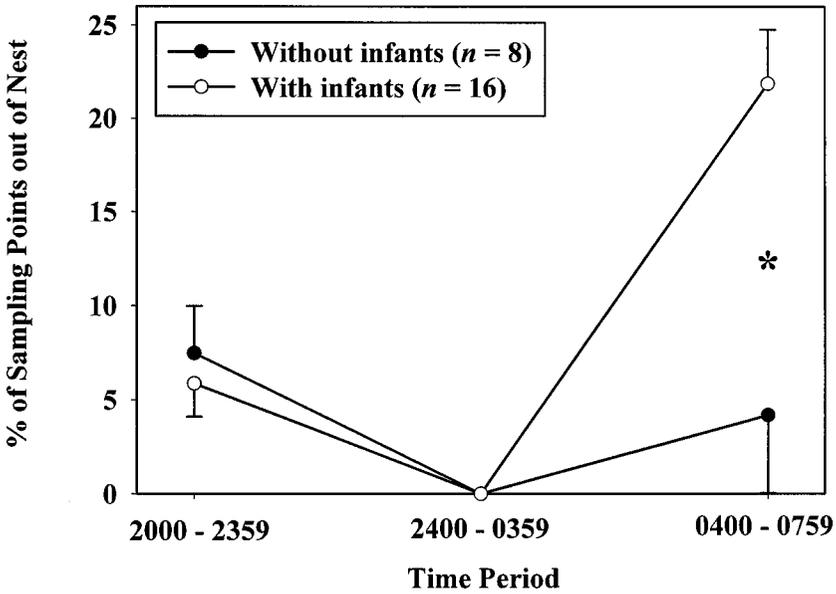


Fig. 2. Mean percentage of sampling points (\pm SEM) that adult marmosets, with and without infants, were out of the nest during late evening, early morning, and late morning hours. * $p < 0.05$

caring for young infants. In fact, mothers rearing infants were awake >3 times as often as mothers without young infants were ($p < 0.001$). Although fathers rearing infants were awake at more sampling points than fathers without infants in their family groups were, the differences were not significant.

Parental time away from the nest was also influenced by the presence of infants (Figure 2). A significant interaction between infant presence/absence and time period ($F(2, 40) = 11.28, p < 0.03$) indicated that the impact of infants on time away from the nest was dependent on the time period. Tests post hoc revealed that parents (both mothers and fathers) with young infants were significantly more likely to leave the nest than parents without infants were ($p < 0.05$), but only during late morning hours (0400 – 0759 h).

Parental Wakefulness and Time Out of the Nest across Infant Development

When we examined parental wakefulness across the first 9 weeks of infant life in a separate set of 5 family groups, we found that parental wakefulness varied by time period and by infant age. Parents were significantly more likely to be awake during the late evening hours (2000 – 2359 h) than during early morning (2400 – 0359 h) or late morning hours

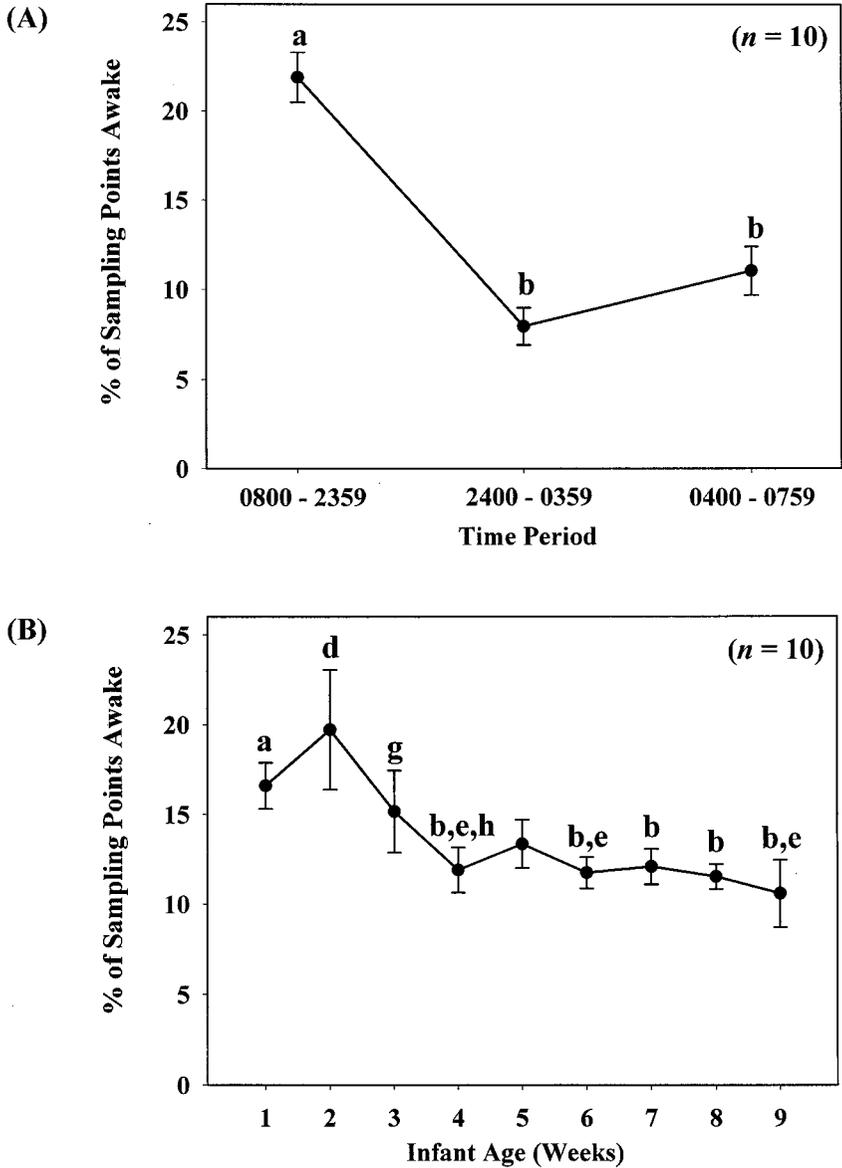


Fig. 3. (A) Mean percentage of sampling points (\pm SEM) that marmosets rearing infants were awake during late evening, early morning, and late morning hours. Time periods demarked by different letters differ significantly from one another, $p < 0.05$. (B) Mean percentage of sampling points (\pm SEM) that marmosets rearing infants were awake across the first 9 weeks of infant life. Weeks demarked by consecutive letters (i.e., a-b, d-e, g-h) differ significantly from one another, $p < 0.05$.

(0400 – 0759 h; Figure 3(A); $F(2, 16) = 41.63$, $p < 0.001$). There was also variability in nighttime wakefulness among postpartum weeks. Mothers and fathers were significantly more likely to be awake during the first 3 weeks of infant life (Figure 3B), during which time infants were most dependent on their caregivers ($F(8, 16) = 3.50$, $p = 0.002$). Nighttime wakefulness at week 1 was significantly greater than at weeks 4, 6, 7, 8, and 9 ($p < 0.05$); nighttime wakefulness at week 2 was significantly greater than at weeks 4, 6, and 9 ($p < 0.05$); wakefulness at week 3 was significantly greater than at week 4 ($p < 0.05$). Although mothers and fathers were more likely to be awake during the first 3 weeks of infant life, when infants were likely to be the most demanding, mothers were awake at significantly more of our sampling points than fathers were across the first 9 weeks of infant life ($F(1, 8) = 6.794$, $p = 0.04$). Mothers were awake at $15.90 \pm 1.05\%$ of the sampling points, while fathers were awake at only $11.35 \pm 0.80\%$ of the sampling points. We also examined parental time away from the nest across the first 9 weeks of infant life. However, no significant effect of sex, infant age, or time period was indicated.

DISCUSSION

Our investigation, the first to examine the nighttime behavior of marmosets in the context of infant care, brings to light several important findings regarding the impact of infant care on sleep patterns in *Callithrix kuhlii*. Mothers rearing infants <2 weeks old were awake >3 times as often as mothers without infants; however, paternal wakefulness, was not significantly affected by the presence of infants. As might be expected, the impact of infants on parental wakefulness was most evident during the first 3 weeks of infant life when infants were most dependent on their caregivers for nutrition, transport, and warmth. Additionally, the mothers rearing infants exhibited more nighttime wakefulness than fathers did across the first 9 weeks of infant life (birth through weaning), despite the fact that callitrichid mothers are often characterized by limited postnatal care of infants, beyond nursing.

In our study, marmoset parents rearing young infants were significantly more likely to leave the nest during the late morning hours (0400 – 0759 h) than adults without infants were. To date, no study has specifically focused on factors that might influence the amount of time after dawn that callitrichid primates spend at their sleeping sites. However, there is evidence, that predator avoidance may be an important influence on decisions to leave a particular sleeping site. Field studies of callitrichid primates indicate that family groups will not enter a sleeping site if they are being observed, and captive

callitrichids are hesitant to enter their nest boxes when human observers are present (Caine *et al.*, 1992). Marmosets and tamarins also behave in ways that appear to reduce the likelihood of detection by predators once they have entered a sleeping site. Captive red-bellied tamarins (*Saguinus labiatus*) had reduced rates of vocalizations in the 30 min before entering the nest box (Caine, 1987). Further, they became nearly silent, yet highly vigilant, once they had entered their nests. All of these reports suggest that callitrichid primates are highly aware of their surroundings when preparing for sleep, and that predator avoidance may influence behavior once a sleeping site has been selected. Although the vocal behavior of callitrichid infants during the night has not been studied, infants can be highly vocal, especially in the context of nursing conflict. Thus, it might be that spending less time at a sleeping site when rearing young infants is an additional form of antipredator behavior.

Energetic demands associated with reproduction and infant care might also influence decisions to leave a sleeping site. In callitrichid family groups, every individual assumes some of the responsibilities, and energetic costs, of caring for infants (e.g., Cleveland and Snowdon, 1984; Goldizen, 1987). Among captive cotton-top tamarins (*Saguinus oedipus*), fathers and male alloparents lose $\leq 11\%$ of their prebirth body weight as they carry infants during the first few weeks of infant life (Achenbach and Snowdon, 2002; Sanchez *et al.*, 1999). Cotton-top mothers lose weight during the first 2 weeks postpartum, when they are most involved in infant care, yet this period of weight loss is followed by intense weight gain that reaches maximal levels during the periovulatory period (Sanchez *et al.*, 1999). Although no direct relationship between weight loss and feeding time has been identified for fathers and male alloparents (Sanchez *et al.*, 1999), callitrichid mothers significantly increase, and in some cases double, their normal energy intakes when lactating (Goldizen, 1987; Kirkwood and Underwood, 1984). Thus, there appear to be tremendous costs incurred during the production and rearing of callitrichid infants, and these costs are not limited to the mother. It may be that callitrichid family groups rearing young infants must leave their sleeping sites early each morning in order to begin foraging to maintain or to replenish their energetic condition.

Our data also indicate that the impact of infants on sleep was greater for mothers than for fathers, during the early postpartum period and even through weaning. This is particularly interesting in light of compelling evidence that, early in the postpartum period, callitrichid females reduce their level of daytime investment in offspring, while fathers exhibit a reciprocal increase in investment (e.g., Bales *et al.*, 2002; Cleveland and Snowdon, 1984; Nunes *et al.*, 2000; Ziegler *et al.*, 1990). Our results show that maternal wakefulness was not limited to the early postpartum period, and that mothers with

infants were awake more often than fathers were across the first 9 weeks of infant life. Contrary to what one might expect, we also found that fathers did not exhibit elevated levels of nighttime wakefulness 3–4 weeks postpartum, during which time they typically assume the responsibility of providing the majority of diurnal care to infants (Nunes *et al.*, 2000). Thus, the presence of infants differentially impacts patterns of sleep in male and female caregivers.

Why might sleep patterns of mothers be more affected by the presence of infants than those of fathers? The differential impact of infants on parental sleep patterns may be related to the type of care being provided at night. As in human mothers (e.g., McKenna *et al.*, 1993; Mosko *et al.*, 1997a), infant movement and arousal, especially when associated with nursing and time on the nipple, occurred immediately before many maternal arousals and awakenings. No form of infant feeding other than nursing occurred during the night, even though marmoset mothers, and to a much greater extent fathers, share food with infants during the day (French and Charlin, 2002). Thus, if infants are being fed during the night, it appears that it must be via nursing. Provided that nursing is the only form of infant care that females cannot share with others, nighttime wakefulness associated with infant nursing may be another maternal energetic demand that ultimately led to the evolution of the cooperative breeding system that typifies callitrichid reproduction.

Elevated nighttime wakefulness may prove to have a profound impact on the energy budgets of callitrichid mothers. Numerous studies indicate that during the night, callitrichid primates exhibit a significant drop in body temperature and resting metabolic rate, i.e., torpor (Hampton, 1973; Hetherington, 1978; Thompson *et al.*, 1994). Distinct behavioral changes accompany the shifts in thermoregulatory and metabolic functioning. Marmosets and tamarins become completely inactive at night, and are difficult to arouse from sleep (Thompson, 1994). The circadian changes in physiology and behavior have been interpreted by Thompson (1992) and Thompson *et al.* (1994) as mechanisms by which callitrichids might be able to conserve some of the energy devoted to thermoregulation, making more energy available for reproduction. However, our focal mothers that were rearing infants and, to a lesser extent, their male counterparts were not completely inactive during the night. We observed general alertness, self- and allo-grooming, as well as infant-directed behavior, e.g., grooming and nursing. While we cannot speak to the thermoregulatory and metabolic functioning of the mothers, it seems likely that they did not experience the energy savings that inactivity, immobility, and torpor might provide. If torpor and behavioral inactivity are indeed mechanisms by which callitrichids shunt energy away from thermoregulation and metabolism, and toward reproduction and infant care,

then females rearing infants may face even greater energetic costs than previously predicated.

Sleep deprivation, be it acute or prolonged, could also have profound impact on the hypothalamic-pituitary-adrenal (HPA) axis functioning of callitrichid mothers. In healthy human males, acute sleep deprivation is associated with elevated plasma cortisol levels the evening following the night of reduced sleep (Leproult *et al.*, 1997), suggesting that sleep deprivation may disrupt normal circadian HPA activity by delaying the decline in cortisol that normally follows the early morning peak. In rats, prolonged sleep deprivation also results in increased HPA activity, which over the long-term is associated with increased body temperature and metabolic rate, impaired immune functioning, and eventually death (Everson, 1995; Rechtschaffen and Bergmann, 1995). Accordingly, mothers caring for infants might have elevated HPA activity as a result of disrupted sleep. A comparison of urinary cortisol excretion in mothers with and without young infants, and examination of the relationship between nighttime wakefulness and cortisol excretion in individual mothers, may allow us to determine whether nighttime wakefulness alters normative HPA function in females.

McKenna *et al.* (1993) suggested that although human mother-infant cosleeping appears to be associated with some cost to a mother's quality of sleep, the effects may enhance infant survivorship. For instance, mother-infant cosleeping may result in mothers being better able to monitor infant behavioral and health status, and to be more responsive to infant stimuli. Increased arousability associated with cosleeping might also promote the development of optimal infant sleeping patterns. Cosleeping could protect against sudden infant death syndrome (SIDS) by maximizing the sensory impact of mothers on their infants or by maintaining increased environmental CO₂ (from maternal respiration), which can stimulate infant respiration (Mosko *et al.*, 1997b). Given these potential benefits for infants in a cosleeping environment and the possible costs to the mother in the form of alterations in maternal sleep architecture, it may well be that a reduced quality and quantity of sleep, while providing care to infants, may represent a form of parental investment. Our work presents preliminary evidence that the sleep patterns of marmoset mothers are significantly affected by the presence of young infants.

Until now, questions about infant care in marmosets and tamarins have been addressed strictly in terms of the behavior that we observe during daylight hours, even though this is only half of the time that mothers are responsible for the well-being and survival of their infants. We have shown that the presence of infants had a greater impact on marmoset mothers than fathers, suggesting that mothers are more involved in infant care than previously realized. Contrarily, fathers were not nearly as involved in nighttime

care as their behavior during the day would suggest. Our findings are particularly exciting as they stimulate new questions, on both proximate and ultimate levels, regarding the expression, allocation, and costs of infant care in callitrichid primates.

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REFERENCES

- Achenbach, G. G., and Snowdon, C. T. (2002). Costs of caregiving: Weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *Int. J. Primatol.* 23(1): 179–189.
- Bales, K., French, J. A., and Dietz, J. M. (2002). Explaining variation in maternal care in a cooperatively breeding mammal. *Anim. Behav.* 63: 453–461.
- Caine, N. G. (1987). Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *Am. J. Primatol.* 12: 241–250.
- Caine, N. G., Potter, M. P., and Mayer, K. E. (1992). Sleeping site selection by captive tamarins (*Saguinus labiatus*). *Ethology* 90: 63–71.
- Cleveland, J., and Snowdon, C. T. (1984). Social development during the first twenty weeks in the cotton-top tamarin (*Saguinus oedipus*). *Anim. Behav.* 32: 432–444.
- Coimbra-Filho, A. F. (1977). Natural shelters of *Leontopithecus rosalia* and some ecological implications. In Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae*, Smithsonian Press, Washington, DC, pp. 79–89.
- Everson, C. A. (1995). Functional consequences of sustained sleep deprivation in the rat. *Behav. Brain Res.* 69: 43–54.
- French, J. A. (1983). Lactation and fertility: An examination of nursing and interbirth intervals in cotton-top tamarins (*Saguinus o. oedipus*). *Folia Primatol.* 40: 276–282.
- French, J. A., Brewer, K. J., Schaffner, C. M., Schalley, J., Hightower-Merritt, D., Smith, T. E., and Bell, S. M. (1996). Urinary steroid and gonadotropin excretion across the reproductive cycle in female Wied's black tufted-ear marmosets (*Callithrix kuhli*). *Am. J. Primatol.* 40: 231–246.
- French, J. A., and Charlin, L. (2002). Food sharing with offspring varies by sex and food quality in marmosets. *Am. J. Primatol.* 57(S1): 25–26.
- Goldizen, A. W. (1987). Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol.* 20: 99–109.
- Hampton, J. K., Jr. (1973). Diurnal heart rate and body temperature in marmosets. *Am. J. Phys. Anthropol.* 38: 339–342.
- Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini): With an Introduction to Primates*, University of Chicago Press, Chicago, 1117 p.
- Hetherington, E. M. (1978). Circadian oscillations of body temperature in the marmoset, *Callithrix jacchus*. *Lab. Anim.* 12: 107–108.

- Keppel, G. (1991). *Design and Analysis: A researcher's Handbook*, Prentice Hall, Englewood Cliffs, NJ, p. 672.
- Kirkwood, J. K., and Underwood, S. J. (1984). Energy requirements of captive cotton-top tamarins (*Saguinus oedipus oedipus*). *Folia Primatol.* 42: 180–187.
- Kleiman, D. G. (1977). Monogamy in mammals. *Q. Rev. Biol.* 52: 39–69.
- Leproult, R., Copinschi, G., Buxton, O., and Van Cauter, E. (1997). Sleep loss results in an elevation in cortisol the next evening. *Sleep* 20: 865–870.
- Lunn, S. F., and McNeilly, A. S. 1982. Failure of lactation to have a consistent effect on interbirth interval in the common marmoset, *Callithrix jacchus jacchus*. *Folia Primatol.* 37: 99–105.
- McKenna, J. J., Thoman, E. B., Anders, T. F., Sadeh, A., Schechtman, V. L., and Glotzbach, S. F. (1993). Infant–parent co-sleeping in an evolutionary perspective: Implications for understanding infant sleep development and the sudden infant death syndrome. *Sleep* 16(3): 263–282.
- Missler, M., Wolff, J. R., Rothe, H., Heger, W., Merker, H. J., Treiber, A., Scheid, R., and Crook, G. A. (1992). Developmental biology of the common marmoset: Proposal for a “Postnatal staging.” *J. Med. Primatol.* 21: 285–298.
- Mosko, S., Richard, C., and McKenna, J. (1997a). Maternal sleep and arousals during bedsharing with infants. *Sleep* 20(2): 142–150.
- Mosko, S., Richard, C., McKenna, J., Drummond, S., and Mukai, D. (1997b). Maternal proximity and infant CO₂ and possible implications for SIDS research. *Am. J. Phys. Anthropol.* 103: 315–328.
- Nunes, S., Fite, J. E., and French, J. A. (2000). Variation in steroid hormones associated with infant-care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Anim. Behav.* 60(6): 857–865.
- Rechtschaffen, A., and Bergmann, B. M. (1995). Sleep deprivation in the rat by the disk-over-water method. *Behav. Brain Res.* 69: 55–63.
- Sanchez, S., Pelaez, F., Gil-Burmann, C., and Kaumanns, W. (1999). Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *Am. J. Primatol.* 48(2): 99–111.
- Santos, C. V., French, J. A., and Otta, E. (1997). Infant carrying behavior in callitrichid primates. *Int. J. Primatol.* 18: 889–908.
- Snowdon, C. T. (1996). Infant care in cooperatively breeding species. *Adv. Stud. Behav.* 25: 643–689.
- Sussman, R. W., and Kinzey, W. G. (1984). The ecological role of the Callitrichidae: A review. *Am. J. Phys. Anthropol.* 64: 419–449.
- Tardif, S., Carson, R. L., and Gangaware, B. L. (1990). Infant-care behavior of mothers and fathers in a communal-care primate, the cotton-top tamarin (*Saguinus oedipus*). *Am. J. Primatol.* 22: 73–85.
- Tardif, S. D., Harrison, M. L., and Simek, M. A. (1993). Communal infant care in marmosets and tamarins: Relation to energetics, ecology, and social organization. In Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*, Oxford University Press, Oxford, pp. 220–234.
- Tardif, S., Jacquish, C., Layne, D., Bales, K., Power, M., Power, R., and Oftedal, O. (1998). Growth variation in common marmoset monkeys (*Callithrix jacchus*) fed a purified diet: Relation to care-giving and weaning behaviors. *Lab. Anim. Sci.* 48: 264–269.
- Thompson, S. D. (1992). Gestation and lactation in small mammals: Basal metabolic rate and the limits of energy use. In Tomasi, T., and Horton, T., (eds.), *Mammalian Energetics*, Comstock, Ithaca, pp. 213–259.
- Thompson, S. D., Powers, M. L., Rutledge, C. E., and Kleiman, D. G. (1994). Energy metabolism and thermoregulation in the golden lion tamarin (*Leontopithecus rosalia*). *Folia Primatol.* 63: 131–143.
- Ziegler, T. E., Savage, A., Scheffler, G., and Snowdon, C. T. (1987). The endocrinology of puberty and reproductive functioning in female cotton-top tamarins (*Saguinus oedipus*) under varying social conditions. *Bio. Reprod.* 37: 618–627.
- Ziegler, T. E., Widowski, T. M., Larson, M. L., and Snowdon, C. T. (1990). Nursing does affect the duration of the post-partum to ovulation interval in cotton-top tamarins (*Saguinus oedipus*). *J. Reprod. Fertil.* 90: 563–570.