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## FAMILY LIFE IN MARMOSETS: CAUSES AND CONSEQUENCES OF VARIATION IN CAREGIVING

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### INTRODUCTION

In most human societies, child development progresses within the context of an intimate social group that has been described as a “family.” There are differences both within and across cultures in the constituents of these family units (e.g., matriarchal kin + offspring vs. a cohabiting man and woman + offspring). Nonetheless, family units share the following common properties: (1) some degree of genetic relatedness among family members, (2) patterns of affiliative and cooperative child-rearing, and (3) co-residence in a common location. The importance of the family environment for development has been recently been highlighted by both professional organizations (e.g., the American Academy of Pediatrics’ “Task Force on the Family;” Schor, 2003) and by funding initiatives (the National Institute of Child Health and Development’s efforts in the Science and Ecology of Early Development, or SEED).

The impact of early social environments, particularly those features involving maternal care, in shaping the developmental trajectories of developing offspring has been elegantly demonstrated in a variety of animal models (see chapters by Maestripieri, Champagne, and Curley in this book). There is also a growing recognition that variation in the normative functioning of human families can have long-lasting and pervasive effects on a variety of developmental

outcomes in individuals that experience these differential early environments. In some cases, poor quality early family life can place children at risk for significant childhood or adult disorders, and higher quality family environments can be protective against these risks. For instance, stress reactivity is modified in children receiving poor quality care early in development (Hane & Fox, 2006; reviews in Gunnar & Quevedo, 2007), and high quality care can overcome the developmental delays in critical brain structures (hippocampus) that derive from low birth weight (Buss *et al.*, 2007). The absence of a father during the early years of a girl’s life can lead to earlier menarche (Draper & Harpending, 1982; Belsky *et al.*, 1991), and father-absence, particularly in the first 5 years of life, is associated with a 2-fold increase in early sexual activity and a 3–5 fold increase in teenage pregnancy (Ellis *et al.*, 2003). Even in families with biological fathers present, the quality of the relationship between fathers and daughters, mothers and daughters, and the quality of the marital relationship itself, is associated with variation in the onset of menarche in girls (Ellis *et al.*, 1999).

Given that families represent important environments that profoundly shape developmental trajectories in offspring, and especially given that considerable normal variation exists in the nature of the early experiences encountered by offspring, it is critical that we understand both the *causes* of variation in the quality and

quantity of care provided to offspring in a family environment, and the *consequences* of this variation for later biobehavioral profiles in adolescents and adults. In the course of this chapter, we will examine both issues in marmosets, who are mostly monogamous, biparental, and family-living primates from the eastern coastal forests of Brazil. We will highlight both endocrine and genetic influences on variation in maternal and paternal care, and document our preliminary evidence of the pervasive and persistent effects of variation in early care for later somatic, physiological, and behavioral functioning in marmosets.

### A PRIMER ON MARMOSET SOCIAL STRUCTURE

Humans share considerable amounts of DNA with the species with which we most recently shared a common ancestor (chimpanzees, *Pan*), and a recent conservative estimate places the overlap at 95% (Britten, 2002). These similarities do not play out, however, in the phenotypic expression of species-specific mating systems. Chimpanzees are known to exhibit mating systems that are characterized by large multimale-multifemale groups, with males mating with multiple females and females mating with multiple males, both within and outside of their social unit, even during a single breeding season (Gagneux *et al.*, 1999). South American primates of the family Callitrichinae (marmosets and tamarins) last shared a common ancestor with *Homo sapiens* somewhere around 35 million years ago (Schrager & Russo, 2003), yet these species exhibit a suite of social and mating characteristics that are remarkably similar to human beings, the details of which are highlighted below.

Marmoset and tamarin social groups are typically extended families made up of 5–15 individuals, and these groups tend to be relatively stable over time (Goldizen, 1987). Social groups are usually comprised of a single breeding adult male and female, perhaps one or more unrelated adults of either sex, and both independent (i.e., juvenile and subadult) and dependent (i.e., infant) offspring of the breeding pair. Strong and persistent social attachments (“pair bonds”) develop between adult male and female heterosexual partners making marmosets and tamarins rare among primates

(Schaffner *et al.*, 1995; Schaffner & French, 2004). These pair bonds are characterized by high rates of affiliative behavior between males and females, including grooming, huddling, food-sharing, and coordination of general activity. Adult males and females are extremely responsive, both behaviorally and physiologically, to threats to the relationship (e.g., separation from a partner: Shepherd & French, 1999; exposure to same-sex competitor: French, *et al.*, 1995; Schaffner & French, 1997).

Marmosets and tamarins also exhibit a cooperative breeding system typified by three defining characteristics: (1) extended residence of offspring within the family group, (2) breeding activity that is typically limited to a single breeding pair, and (3) alloparental care (i.e., care provided to infants by individuals other than a parent; French, 1997). Unlike most mammals, in which dispersal of offspring from the natal group by one or both sexes occurs around the time of puberty (Chepko-Sade & Halpin, 1987), subadult and adult marmoset offspring remain in the natal group, sometimes for years. It is rare, however, for these adult-aged offspring to engage in breeding attempts. In some cases, adult-aged daughters living in their natal family are endocrinologically suppressed and fail to exhibit normal ovarian cycles (see review in French, 1997), but in other cases, daughters and subordinates are reproductively capable but fail to engage in sexual behavior (Smith *et al.*, 1997; Saltzman *et al.*, 2004). Likewise, subordinate males and sons living in natal groups do not routinely engage in sexual activity, although they are capable of copulating with an unrelated female when given an opportunity, and have levels of testosterone and luteinizing hormone (LH) sufficient to support spermatogenesis and sexual behavior (Baker *et al.*, 1999).

Besides delayed dispersal and cooperative breeding, the most crucial aspect of marmoset reproductive biology from the perspective of this chapter is cooperative infant care. Marmosets typically produce fraternal twins that are cared for by *all* group members, including fathers and older offspring living in the family group (Tardif, 1997). This trait is shared by all species of marmosets and tamarins, although there are subtle differences among species and genera in the distribution and timing of parental effort by mothers, fathers, and alloparents (Santos *et al.*, 1997; Tardif, 1997). Patterns of caregiving provided to infants include licking and grooming, food-sharing and provisioning, play,

protection and contact-comfort, and, in the case of breeding females, nursing. But by far the most dramatic and energetically expensive component of offspring care is infant carrying and transport. At birth, the cumulative weight of a twin litter can constitute 15–25% of adult body weight (French, 1997), and by the time weaning is complete at 12 weeks of age, the combined weight of twins approaches 100% of adult body weight. Caregivers that are transporting offspring show reductions in time spent feeding and foraging (Price, 1992) and can lose 10% of their body weight during times of high carrying activity (Sanchez *et al.*, 1999), suggesting that there are real energetic and metabolic costs associated with offspring carrying in marmosets. For mothers, the costs of carrying are compounded by two additional energetic and metabolic demands. First, via lactation mothers provide their rapidly growing offspring with milk that is rich in energy from crude protein (Power *et al.*, 2002). Second, mothers are often pregnant with a new litter (in which they are beginning the investment of 15–25% of their body weight) on the first postpartum ovulation. In our colony, approximately 85% of first postpartum ovulations in marmosets are conceptive ovulations, and these occur 7–14 days postpartum (French *et al.*, 1996).

The Callitrichid Research Center at the University of Nebraska at Omaha has focused on family life in two species of marmosets, the black tufted-ear marmoset (*Callithrix kublii*) and more recently, the white-faced marmoset (*C. geoffroyi*). Our animals are housed in large enclosures that contain naturalistic features such as branches and vines, nest boxes, and simulated foraging sites. Most of the work described in this chapter involves behavioral observations of normal, undisturbed parents and offspring, and all of our endocrine work is conducted on urine samples that are collected non-invasively (marmosets are trained to provide first-void urine samples upon arising in the morning; French *et al.*, 1996).

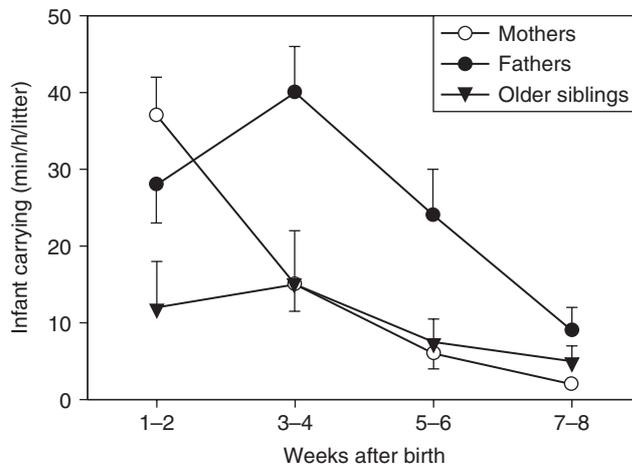
### ENDOCRINE CORRELATES OF VARIATION IN PARENTAL CARE

Our approach to evaluating the links between variation in endocrine states and the expression of parental care is strongly shaped by models that integrate behavioral endocrinology

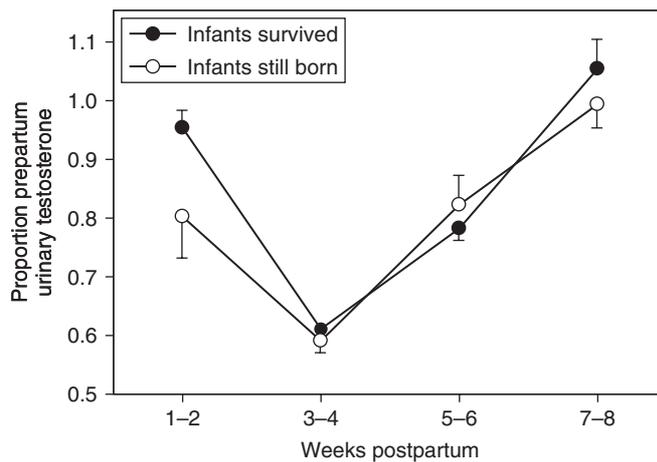
and behavioral ecology, particularly trade-off models. These models (e.g., Wingfield *et al.*, 1990; Ketterson & Nolan, 1999; Zera & Harshman, 2001; Ketterson *et al.*, 2005) posit that hormones represent important proximate determinants of life history “decisions,” mediating trade-offs between alternative behavioral or reproductive choices. We have focused specifically on the hypothesis that androgenic hormones such as testosterone mediate shifts in investments between parental effort (caring for current offspring) vs. mating effort (time and energy directed toward producing future offspring). There is considerable support for this hypothesis in a wide variety of vertebrate species (review in Ziegler, 2000), but there are also notable exceptions (see contributions by Marler in this book).

In the marmoset, we first addressed the question of how parental labor is divided among group members during different phases of the infants’ early life. Marmoset infants are dependent on caregivers for transport for the first 2 months of life, so we recorded rates of carrying effort during this time. The overall effort by mothers, fathers, and juvenile helpers during the 8-week period after birth is shown in Figure 30.1. During the first 2 weeks of postpartum infant life, mothers are the primary offspring caregivers, but show a significant decrease in carrying effort during weeks 3–4 postpartum. This reduction in female care is accompanied by an increase in offspring care by fathers, who exhibit a 40% increase in carrying effort from weeks 1–2 to weeks 3–4. In a typical marmoset family, fathers are therefore the primary caregivers during this period of infant life, and continue to be the primary caregivers throughout the period of infant dependence (although their effort, like other caregivers, decreases as the infants grow older and acquire more independence). Helpers in the group (older siblings of the infants) carry little early in development, but are involved at levels similar to adult female in weeks 3–8. When looking at the pattern of change in parental roles in the social group, then, there are two important transitional elements in parental effort. Males become much *more* engaged in parental care in weeks 3–4, while at the same time, females become much *less* involved in parental care at the same point in time.

To address whether changes in androgens were temporally associated with variation in paternal effort (as predicted by the trade-off



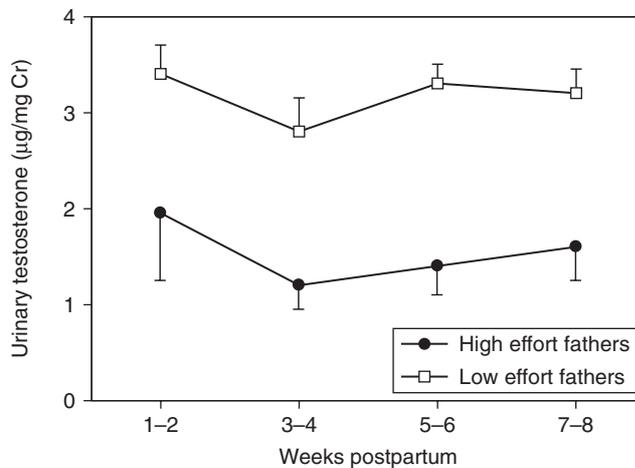
**FIGURE 30.1** Rates of infant carrying throughout the first 8 weeks of infant life by the three major classes of marmoset caregivers. Error bars indicate  $\pm$  SEM.



**FIGURE 30.2** Changes in urinary testosterone excretion in male marmosets in the first 8 weeks of infant life. Values are expressed as a proportion of prepartum hormone concentrations. (Source: Modified from Nunes *et al.*, 2000.)

hypothesis), we monitored changes in testosterone excretion in males across this 8-week period (Nunes *et al.*, 2000). We collected data on a set of males who were actively engaged in parental care with a litter of twins, and on a second group of males whose infants were stillborn or who died of natural causes in the first 2 days of life. These two groups allowed us to determine whether any endocrine changes we observed in males were specifically associated with and potentially triggered by actively engaging in paternal care, or were cued by exposure

to cues from pregnant females and/or the events associated with parturition. We found that relative to prepartum baseline testosterone levels, testosterone levels in males dropped slightly during the first 2 weeks postpartum, but then dropped to 60% of baseline levels during the period of maximal male care (weeks 3–4; Figure 30.2). As male carrying effort decreases in weeks 4–8, testosterone levels returned to baseline prepartum concentrations. Similar profiles were noted in males whose infants died within 2 days of birth and in males who reared infants



**FIGURE 30.3** Urinary testosterone excretion in males that engaged in high levels of paternal care (high effort) vs. males that engaged in lower levels of paternal care (low effort). (Source: Modified from Nunes *et al.*, 2001.)

throughout the 8-week period after birth. This suggests that stimuli associated with parturition or the short-term presence of neonates, initiates an endogenous timing mechanism that facilitates later parental care, regardless of the continued presence of live offspring (see similar results in parental penguins: Lormée *et al.*, 1998). In some cases fathers actively consume the placentas associated with the twin litters (personal observations). The consumption of a steroid-rich tissue like the placenta may initiate long-term endocrine changes in males. Alternatively, cues for the change in endocrine status in males may arise from sources other than the infants, including olfactory cues emanating from ovulatory or newly pregnant females (Ziegler *et al.*, 1993), or behaviorally induced changes in endocrine activity associated with the termination of female sexual attractiveness and receptivity.

Our analyses also revealed that previous experience with infants shapes the extent of testosterone suppression in the presence of infants. With age of male, group size, and other potentially confounding variables controlled, males with greater levels of previous infant experience (either as helpers or as fathers) showed significantly lower concentrations of testosterone postpartum than males with less experience. This finding suggests critical interactions between experience as a parent and the regulation of gonadal steroidogenesis, an interaction that may also occur in the relationship between

prolactin and parental care in other species of marmosets and tamarins (Ziegler *et al.*, 1996).

Our second study on paternal male marmosets (Nunes *et al.*, 2001) addressed the possibility that individual differences in male paternal effort were associated with variation in gonadal steroid concentrations. We identified a population of males that carried infants at high rates (high effort males; males that carried on average 33 min/h) and a population that carried infants at low rates (low effort; less than 15 min carrying/h), and monitored patterns of paternal care and hormone excretion across two successive litters of twin offspring. While these two populations of males did not differ on a host of demographic and experiential measures (including age, previous experience, size of groups, length of pairing with the female), there were profound differences between males in endocrine profiles during the postpartum period. High effort males had significantly lower concentrations of testosterone than low effort males throughout the period of infant dependence on caregiving (Figure 30.3). The magnitude of the difference between these subsets of males is remarkable – fathers that engage in less paternal care have levels of excreted testosterone that were 2-fold higher than levels in fathers that engage in substantial parental care. It is of interest to note, however, that both populations of males showed reductions in urinary testosterone excretion during weeks 3–4 of infant life, which replicated

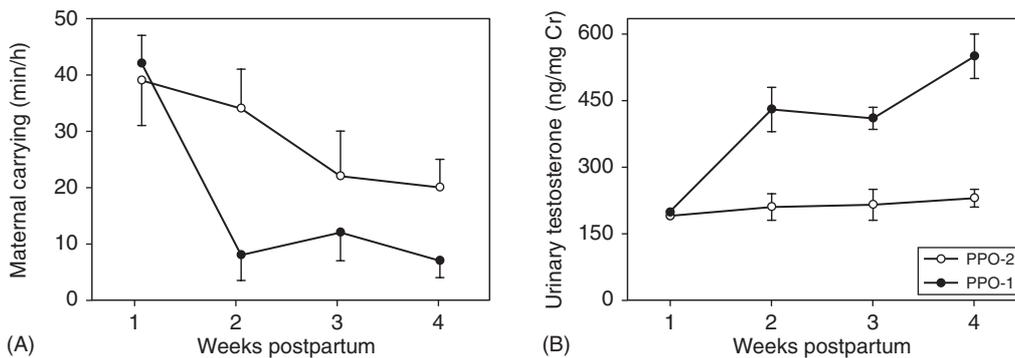
the effect we had observed earlier (Nunes *et al.*, 2000). Cortisol (CORT) also varied as a function of male parental effort, with low effort males showing dramatically higher levels than high effort males, especially in the first 2 weeks postpartum. We also noted an experience effect on hormones levels in this study, with fathers (both high and low effort) caring for their second set of infants having significantly lower testosterone than they did while caring for their first set. Thus, the timing of changes in testosterone in males across the period of infant dependence (low levels during high paternal effort) and the endocrine differences between males that vary in paternal effort (highly involved fathers have lower testosterone) are observations consistent with the trade-off hypothesis.

### Androgens and Variation in Maternal Care

As seen in Figure 30.1, there is a dramatic transition in amount of infant care provided by the mother, beginning in the third week of infant life. Mothers exhibit an almost 4-fold reduction in carrying infants at this time, although they are still actively nursing their offspring during the short period of time they are also carrying infants. We know that the timing and magnitude of this reduction in maternal care is associated with at least one demographic variable and one reproductive variable (Fite, *et al.*, 2005b). First, females reduce their carrying effort more dramatically during this time when there are

helpers in the group than when no helpers are available. Second, female marmosets who conceive in the first postpartum ovulation (7–14 days postpartum) immediately reduce their carrying effort in the current set of infants while females who conceive on the second or third postpartum ovulation (30–50 days postpartum) exhibit a much more gradual decline in carrying efforts (Figure 30.4(A)). The reduction in care in the first instance is rapid and dramatic – females reduce infant carrying from ~40 min/h to <10 min/h if they conceive on the first postpartum ovulation. We have suggested that female marmosets are remarkably “opportunistic,” reducing maternal effort when they can (additional helpers) or when they have to (in the face of combined lactational and gestational energetic demand). Thus, females appear to facultatively adjust caregiving effort as a function of energetic and social contexts.

There is growing interest in the role of heterotypical gonadal steroid (i.e., androgens in females and estrogens in males) in the regulating of sociosexual behavior, including paternal care (Schum & Wynne-Edwards, 2004; Ketterson *et al.*, 2005). We evaluated the possibility that androgens may play a role in regulating maternal responsiveness, in a manner similar to the pattern suggested by our data on male parental effort. Unpublished data collected on our marmosets by Erin Kinnally revealed that marmoset mothers (experienced and inexperienced) exhibited significant increases in urinary testosterone in weeks 3–4 postpartum, which corresponds exactly to the time at which females exhibit a 4-fold reduction in their efforts in transporting



**FIGURE 30.4** (A) Maternal care of offspring and (B) patterns of urinary testosterone excretion in female marmosets during the first 4 weeks postpartum. PPO-1, females conceived on their first postpartum ovulation; PPO-2, females conceived on the second or later postpartum ovulation. Cycle length in *Callithrix* is approximately 24 days in length. (Source: Modified from French *et al.*, 1996.)

offspring (see Figure 30.1). We hypothesized, based on these data, that elevated androgens may represent a proximate signal that reduces maternal investment in current offspring (at least those features, like offspring transport, that can be shifted to individuals other than the mother), thereby allowing greater investment in the future offspring the female is beginning to gestate. Where do these high levels of androgens come from in females? Previous work in a variety of mammals (dogs, baboons, humans) has shown that one of the most distinctive differences between conceptive vs. non-conceptive ovarian cycles is the rapid and dramatic rise in testosterone associated with conceptive cycles, presumably of ovarian origin (Castracane & Goldzieher, 1983; Concannon & Castracane, 1985; Castracane *et al.*, 1998).

Once again, variation in marmoset biology allowed us to test the androgen trade-off hypothesis in females. Most females conceive on the first postpartum ovulation, but on some occasions they do not. We (Fite, *et al.*, 2005a) identified a set of females who on one occasion had a surviving litter of twins and subsequently conceived on the first postpartum ovulation, while on another occasion produced a set of twins, but did not have a conceptive ovarian cycle until the second or third postpartum ovulation. We monitored ovarian steroids (estrogen and progesterone metabolites), and testosterone levels in the postpartum period, and noted levels of maternal carrying effort. Our data demonstrate that traditional ovarian steroids do not change dramatically at conception, but that urinary androgen concentrations in females rise dramatically in the conceptive, but not in the non-conceptive luteal phase. The results are consistent with our hypothesis – females that conceived on the first postpartum ovulation exhibited elevations in testosterone levels, coincident with a reduction in maternal carrying effort (Figure 30.4(B)). When females did not conceive on the first postpartum ovulation, androgens did not rise and maternal effort remained high. The temporal relationship between elevated androgen levels and reduced maternal care in conceptive mothers is supported by analyses that assess the relationship between maternal androgen and carrying efforts. The correlation between androgen levels and carrying effort is negative and highly significant for all data combined ( $p < 0.002$ ) and also for individual females (i.e., higher androgen levels were associated with reduced carrying rates).

Together, our data on androgens and parental care in marmoset families point to an integrated system of hormone–behavior interactions that helps to regulate the timing of parental effort among adult caregivers in marmoset social groups. Male endocrinology varies in ways that reflect their dual roles as breeding partners and as caregivers. In the immediate postpartum phase, testosterone titers in males remain high, during which time males defer to females with regard to infant care, but actively monitor the female's reproductive state and engage in sexual behavior in the postpartum ovulation. Following the postpartum ovulation and mating, testosterone titers fall and males become more nurturant, and indeed become the primary caregivers for infants within the family group. In females, elevated androgens are associated with a reduction in carrying effort for the current litter, presumably conserving energetic resources for the expensive task of producing a future litter of offspring. These results lend support to the growing appreciation that hormones mediate important life history decisions, mating effort vs. parental effort in males, and current vs. future offspring in females.

### GENETIC CHIMERISM AND EVOCATIVE GENETIC EFFECTS ON PARENTAL CARE

It is not uncommon for parents and offspring to have correlated traits, such as temperament. To the extent that these traits display some heritability, traditional quantitative geneticists would suggest that parents and children are similar because of a Mendelian transmission of relevant alleles across generations. A more modern approach, however, suggests that some of the “heritable” covariance may be attributed to evocative effects – the differential solicitation of parental behavior that is evoked by genetically based social and behavior phenotypes in children. For example, when children inherit certain behavioral phenotypes (e.g., distractable or resistive), they tend to evoke a certain parental style (e.g., authoritarian). On the other hand, a cooperative child will evoke a different pattern from the same parents (e.g., laissez-faire: see reviews in Collins *et al.*, 2000; Maccoby, 2000; Reiss & Neiderhiser, 2000; Neiderhiser, this book). Knowledge of the nature of these genetic effects contributes to our understanding of normative gene–environment

interactions, but in addition, these evocative effects also speak directly to important health-related outcomes. For instance, adopted children reported to be at genetic risk for antisocial behavior (based on biological mothers' self-reported history of antisocial behavior) elicit higher levels of negative parenting from adoptive parents than children not at genetic risk (Ge *et al.*, 1996; O'Connor *et al.*, 1998).

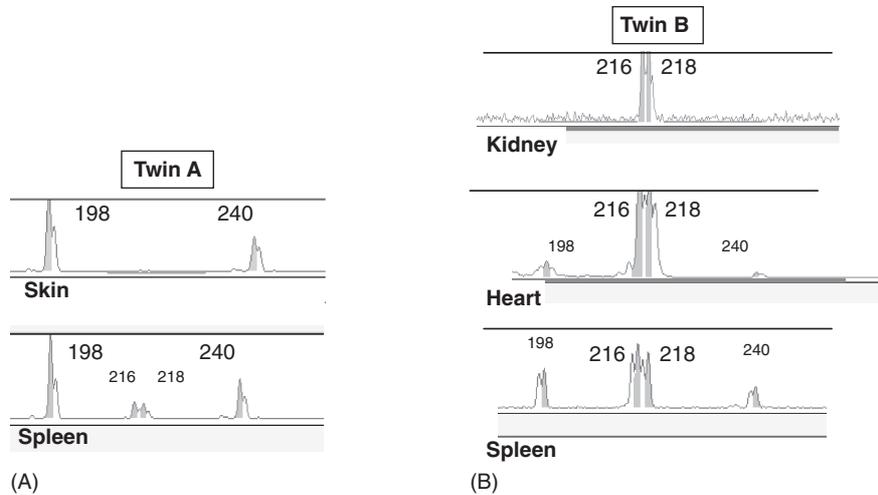
We have discovered what may, in fact, be an important evocative genetic effect in marmosets, in the form of genetic chimerism. A genetic chimera is a unitary organism that is composed of cells that contain alleles from differing genomic lineages. Naturally occurring mammalian chimeras have been known for almost a century, and the most common example is free-martinism in cattle (Lillie, 1917). Fetal female cows that have a male co-twin are rendered sterile, because the presence of chimeric XY-containing cells in the female fetus masculinizes the female's genitalia (see recent review in Capel & Coveney, 2005). It was recently reported that women who have given birth to one or more children maintain cell lines that express the genotype of their offspring (these cells contain alleles that derive from the child's father as well as the mother, and hence are non-self alleles for the mother; Maloney *et al.*, 1999). These chimeric cells can persist in the maternal circulation for decades, and include CD34(+) and CD38(+) cells and other components of the immune system. Chimerism has been noted at an incidence of approximately 33% of healthy mothers, but the incidence is higher in women with autoimmune disorders (Evans *et al.*, 1999), suggesting that, as in free-martinism, there may be moderate to strong costs associated with chimerism.

In marmosets, in contrast, the entire sequence of placentation and embryonic development appears to be designed specifically to produce genetic chimeras of the fraternal twins that develop *in utero*. Early in embryonic development, the placental anastomoses fuse and form a single chorion (Wislocki, 1932). Fusion of the twins' placentas begins on day 19 and is complete by day 29, forming a single chorion with anastomoses connecting the embryos which are still at a presomite stage in development (Merker *et al.*, 1988; Missler *et al.*, 1992). The fusion of the chorions and a delay in embryonic development at this stage allows the exchange of embryonic stem cells via blood flow between the twins (Benirshke *et al.*, 1962;

Benirshke & Brownhill, 1963). As a result, the infants are genetic chimeras with tissues derived from self and sibling embryonic cell lineages. A similar phenomenon occurs with rare frequency in humans. A recent report on dizygous (fraternal) male and female human twins sharing a single placental chorion demonstrated chimerism in blood-derived products, including the presence of XY-bearing cells in the female, and XX-bearing cells in the male (Souter *et al.*, 2003). While there is little doubt that tissues derived from hematopoietic origin are universally chimeric in marmosets (Benirshke *et al.*, 1962; Gengozian *et al.*, 1964), the existence of chimeric cells in non-hematopoietic tissues, including germ-line cells such as sperm and egg is controversial (Gengozian *et al.*, 1980), and has not been systematically evaluated.

Our recent analyses of chimerism in marmosets (Ross, *et al.*, 2007) were the first to use modern molecular genetic tools to examine chimerism in a variety of tissues and with a number of microsatellite DNA primers. Multiple tissue samples were collected from living marmosets and from archived tissues from deceased marmosets in our colony. This colony has been painstakingly pedigreed since its origination in 1991, and there were no ambiguities in paternity in any of the offspring produced in our lab. Samples were blindly coded, DNA was extracted and amplified, and genotypes were determined for five marmoset markers. Majority rule was used to determine "self" genotype (i.e., those alleles that were likely to be inherited vertically from each parent) and "sibling" alleles (those alleles acquired *in utero* from the sibling via horizontal transmission). The ABI scans in Figure 30.5 show typical data for a single marker (CK2). Skin tissue from Twin A is clearly heterozygous at this locus (198/240) and kidney tissue from Twin B is also heterozygous, but with different alleles (216/218). DNA from Twin A's spleen still shows evidence of self alleles at 198/240, but some proportion of the DNA extracted from Twin A's spleen contains alleles expressed by Twin B. Likewise, DNA from Twin B's heart tissue contains a high signal of self alleles (216/218), but the extracted DNA also contains alleles from Twin A.

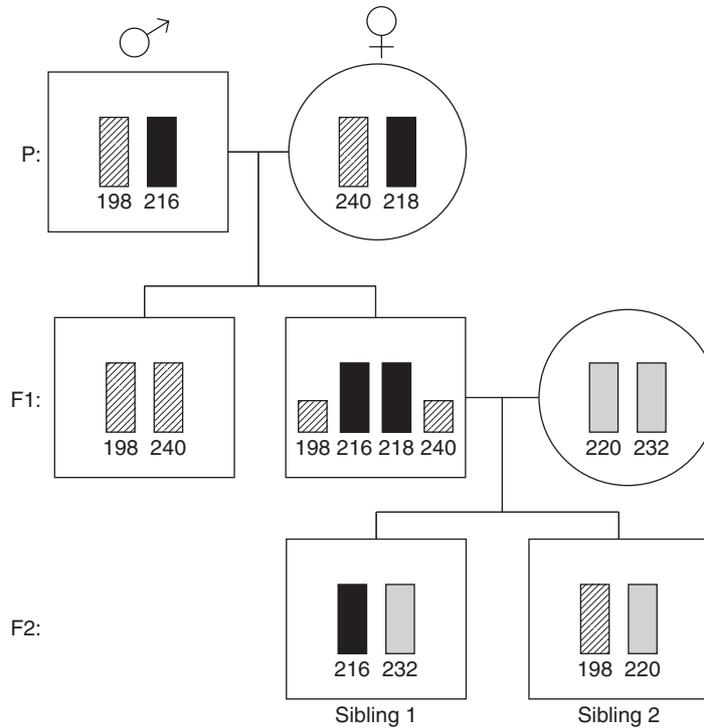
Although the incidence of chimeric tissue varied among tissue types, every tissue sampled showed evidence of chimerism, perhaps most surprisingly (and importantly) in the germ line. In harvested and purified sperm samples collected from males, 57.1% of the samples



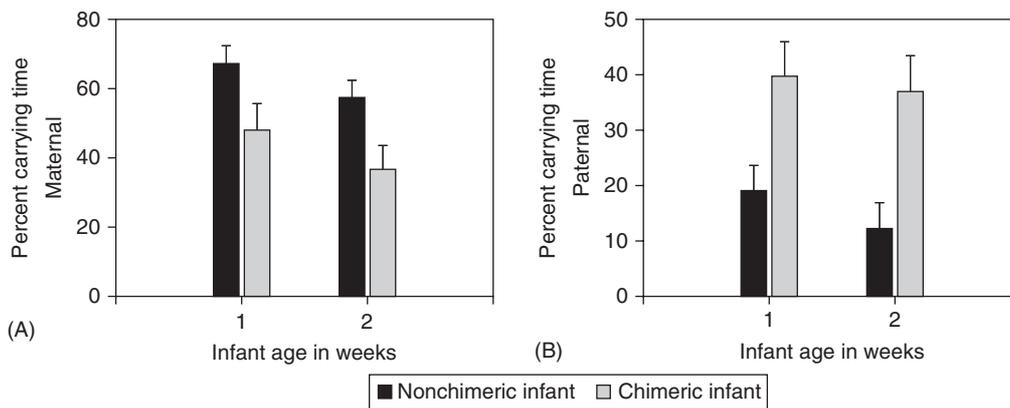
**FIGURE 30.5** Genotype data for two marmoset co-twins. Twin A has a designated self genotype of 198/240 for this locus (CK2) as determined by majority rule, and twin B has a designated self genotype of 216/218. This figure also demonstrates that Twin A is chimeric for spleen tissue and nonchimeric for skin, whereas Twin B is chimeric for heart and spleen tissue. (Source: Modified and reprinted with permission from Ross *et al.*, 2007.)

contained chimeric sperm (i.e., expressed an allele associated with the intrauterine sibling), and we estimated that 1 out of every 10 sperm cells (~10%) contain chimeric alleles. From a genetic perspective, what is most intriguing is that we have demonstrated that offspring can be sired by males with chimeric sperm that males inherited horizontally from their co-twins. The genealogy in Figure 30.6 demonstrates this point. The parental generation (P) is heterozygous for marker CK2. One of the sons in F1 inherits allele 198 from the father and 240 from the mother. The second son inherits 216 from father and 218 from mother (as determined by majority rule), but also expresses 198 and 240 as alleles contained in sibling cells. This son is paired with a female from another family line who has unique alleles at CK2. Sibling 1 in the F2 generation inherits 216 from father and 232 from mother, but Sibling 2 in F2 inherits the chimeric allele 198 from the father and 220 from the mother. This outcome can only arise if the “father” fertilized the egg with a sperm that was derived from embryonic stem cells that were passed to the male via placental anastomoses with his intrauterine co-twin. Of 34 twin sets evaluated in our analyses, five instances of transmission of chimeric alleles across generations were noted. This phenomenon has clear implications for coefficients of relatedness within marmoset groups.

From a behavioral perspective, it seemed likely that marmoset infants that were chimeric might be treated differently by caregivers, since they may differentially express phenotypic cues regarding relatedness. For example, in generation F1 above, the male marmoset on the far left expresses only one copy of each allele from the parents, while the son in the middle of the genealogy potentially expresses phenotypic products associated with both sets of alleles from each parent. To evaluate the possibility that offspring may be treated differentially, we divided marmoset infants into two categories: those that were chimeric for epithelial tissue ( $n = 10$ ) and those determined to be nonchimeric for epithelial tissue ( $n = 20$ ). We compared rates at which each of these classes of infants was carried by mothers vs. fathers during the first 2 weeks of infant life, a period of time during which the mother is typically the primary caregiver (Fite & French, 2000; Nunes *et al.*, 2000, 2001; Fite *et al.* 2005b). Figure 30.7 shows the percentage of carrying offspring by the mothers and fathers, and it is clear that at both 1 and 2 weeks of infant age, fathers carry chimeric infants at 2-fold or higher rates in the first 2 weeks of life than nonchimeric infants. As shown earlier, males are normally not the primary caregivers during this period of time, but if infants possess chimeric alleles in epithelial tissue, fathers appear to be



**FIGURE 30.6** Example of vertical transmission of chimeric alleles acquired from a sibling co-twin. The parental pair (P) produced two male offspring that had different self genotypes, but one son expressed alleles born by its co-twin (198/240). This son was paired with a female with a different genotype, and Sibling 2 in the F2 generation bears an allele that was acquired by its father (F1) from its male co-twin. (Source: Modified and reprinted with permission from Ross *et al.*, 2007.)



**FIGURE 30.7** Patterns of infant care by mothers (A) and fathers (B) for infants whose epithelial tissue was chimeric (i.e., displayed self alleles plus at least one sibling allele) vs. those infants whose epithelial tissue was nonchimeric (contained self alleles only). Mothers with chimeric infants carry significantly less than those with nonchimeric infants ( $p = 0.01$ ), and fathers with chimeric infants carry significantly more than those with nonchimeric infants ( $p = 0.002$ ). (Source: Modified and reprinted with permission from Ross *et al.*, 2007.)

particularly attracted to these infants and carry them significantly more than they do nonchimeric infants. Mothers show a slight reduction in the percent of time they carry chimeric infants, but the differences are not as dramatic as the differences displayed by male marmosets toward chimeric vs. nonchimeric offspring. In this dataset, we only recorded carrying effort, and we have no other quantitative information regarding attraction to or aversion from infants on the part of either mothers or fathers. Thus, our data do not allow us to assess whether higher rates of paternal carrying resulted from greater male interest in chimeric infants (e.g., higher rates of transfer and attempted transfer to males, increased sniffing and anogenital licking, shorter latency to retrieve) or, alternatively, the possibility that mothers find chimeric infants less attractive or even aversive and engage in higher rates of rejection, attempted rejections, and infant removals, which would lead to higher male care as a consequence. We are currently addressing this question with more detailed behavioral protocols that will allow us to answer these critical questions regarding the link between chimeric status and the quality, quantity, and distribution of parental caregiving activities within the context of a family system. Differential paternal responsiveness based on the genotype of offspring would appear to be an example of a profound evocative effect in parental care.

## CONSEQUENCES OF VARIATION IN EARLY PARENTAL CARE

### Impact of Variation in Early Care on Baseline HPA Function and Pubertal Maturation

Adverse or inappropriate maternal care is known to have profound influences on the development of primate offspring. Compelling evidence on this point is available from experimental studies that involve maternal deprivation or separation (Dettling *et al.*, 2002a,b; Sanchez, 2006) or studies of fairly intense maternal abuse and neglect (Maestripieri, 2005; this book). Our approach to addressing the question of early experiences and epigenesis, in contrast, is to examine the impact of *natural* variation in normative early offspring care on subsequent development. Marmoset infants are,

on the whole, remarkably well-cared for during the first 2 weeks of life. It is rare to have a set of twin infants that are not carried by one or another caregiver 100% of the time. However, there are significant differences among family groups and even between co-twins in the identity of the caregiver that provides the majority of care during the first 2 weeks of life.

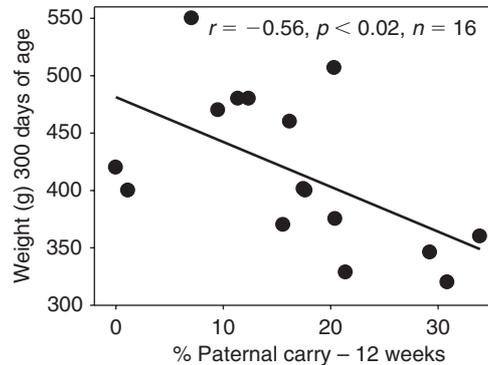
We have recently completed an analysis of the impact of this variation on baseline set-points in the hypothalamic–pituitary–adrenal (HPA) axis and on the onset of reproductive function (French *et al.*, under review). We studied the development of 12 marmoset infants in family groups where mothers, fathers, and alloparents were present and could provide offspring care. Eleven of the 12 infants were on caregivers 100% of observations, while the 12th was on caregiver 97.3% of observations. Nonetheless, differences in the kinds of experience offspring had during the first 2 weeks of life had profound influences on later physiological markers, in sex-specific ways. First, the variation in the extent to which mothers carried daughters was a significant predictor of age at onset of the first signs of ovarian activity in daughters. The first ovulatory cycle was documented by monitoring patterns of progesterone metabolites in urine samples. Daughters that received more care from mothers *in the first 2 weeks of postnatal life* had earlier pubertal timing than daughters who received less care from mothers ( $r = -0.99$ ,  $p < 0.001$ ). Variation in early caregiving also influenced baseline function in the HPA axis, as 12-month-old daughters who were carried less frequently by mothers in the first 2 weeks of life exhibited higher baseline levels of urinary CORT ( $r = -0.84$ ,  $p < 0.03$ ). When we performed regression analysis on maternal caregiving and CORT levels on pubertal timing, the overall model was significant, explaining 99.2% of variation in pubertal timing. However, removing baseline HPA activity using backward selection did not produce a significant change in  $R^2$ , suggesting that the relationship between maternal care and pubertal timing was not mediated by baseline HPA activity at 12 months of age.

Like daughters, sons also received differential care during early life. Also like females, pubertal processes appeared to be influenced by early care – in this case, variation in the amount of care sons received from their fathers. Unlike a discrete event like first ovulation in females,

the development of puberty in males is a more continuous process. We estimated degree of pubertal maturation by measuring individual differences in urinary testosterone (T) in males at 12 months of age (the peripubertal stage in marmosets). Sons that were carried by fathers more in the first 2 weeks of life had lower levels of urinary testosterone at 12 months of age than sons that were carried less frequently by the father ( $r = 0.83$ ,  $p < 0.03$ ). This effect appears to be specific to father–son caregiving, since neither variation in caregiving by mothers nor older siblings was correlated with peripubertal testosterone levels in sons. Paternal caregiving was not associated with variation in HPA function at 12 months of age in sons, suggesting that paternal influences on pubertal process in sons is independent of simultaneous activation of the stress system. While we do not have data on early HPA function in infants (i.e., during the first 2 weeks of life while they receive differential caregiving), it may be that differential care may influence pubertal processes via differential early activation of the HPA axis. Infant marmosets are known to be hypercortisolemic (Pryce *et al.*, 2002), and differential early family experiences can alter HPA function (Dettling *et al.*, 2007).

### Differential Early Care and Somatic Development in Marmosets

In addition to endocrine function and sexual maturation, we have also been exploring the impact of differential early care on infant and juvenile somatic development. We collect complete somatic measurements on all infants born into our colony on a regular basis, beginning at the age of 2 days and continuing throughout development until adulthood (540 days of age). Our preliminary analyses of somatic growth show that variation in early care influences important components of physical growth. High levels of paternal care early in development have negative consequences for somatic growth. As seen in Figure 30.8, those offspring that receive more paternal care in the first 12 weeks of life weigh less at 300 days of age than those who receive less paternal care, and these differences persist until 480 days of age. Further, several of our measures of physical “robustness” (e.g., chest, abdominal, and thigh circumference) are negatively correlated with early paternal care, even at age

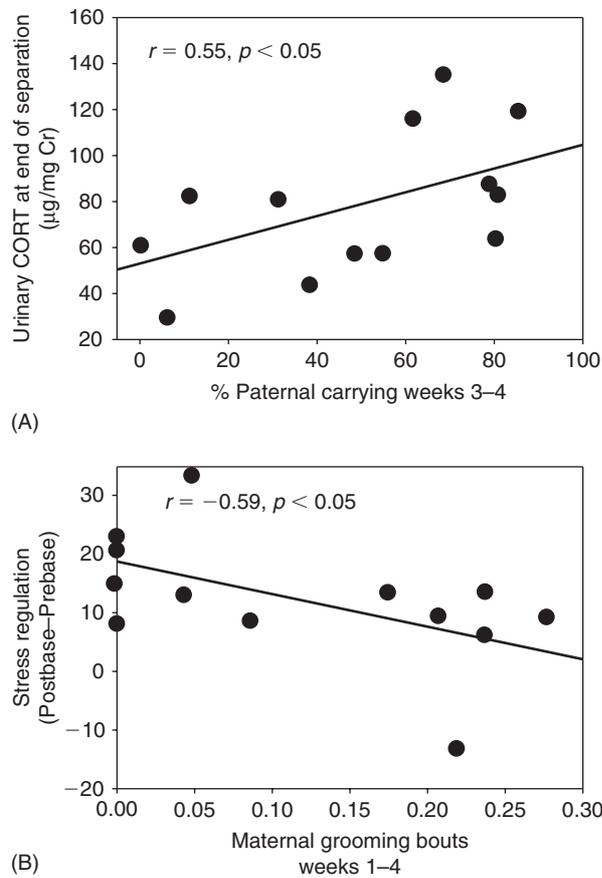


**FIGURE 30.8** Weights of juvenile marmosets at 300 days of age varies as a function of the proportion of time they were carried by fathers during the first 12 weeks of life.

points as distant as 540 days. These effects do not appear to be caused by a lack of opportunity to nurse during this early period, since differences in maternal carrying effort (and hence infant ability to gain access to nursing) are not correlated with somatic outcomes later in life.

### Differential Early Care and Stress Reactivity in Juvenile Marmosets

We hypothesized that variation in early care in marmosets would differentially program later function in the HPA axis. Our preliminary data show that important parameters of stress reactivity in juvenile marmosets are differentially expressed based on early care (Burrell & French, 2007). We have analyzed stress reactivity at 6 months of age (the juvenile stage) for 14 marmosets (7 male, 7 female) who received differential care early in life. Baseline urine samples were collected, and then juveniles were separated from their natal group and housed in a novel cage in an unfamiliar environment – thus, the stressor constituted both social separation and exposure to environmental novelty. Several aspects of the dynamics of the stress response, assessed by measuring excreted CORT in non-invasively collected urine samples, were affected by differential maternal and paternal care in the first month of life. Variation in paternal care affected stress “reactivity,” as shown in Figure 30.9(A), as measured by maximum CORT levels at the



**FIGURE 30.9** Differential early family care of marmoset infants alters stress responsivity: (A) 6-month-old marmosets that had received greater paternal carrying during weeks 3–4 of life show higher maximum CORT titers in response to separation and novelty exposure; (B) 6-month-old marmosets that had received more maternal grooming bouts early in life were more likely to return to baseline levels of CORT after a psychosocial stressor than marmosets who received fewer grooming bouts.

end of the 8-h separation. Juveniles that had been carried at high rates by fathers in the second 2-week period in postnatal life had higher CORT at the end of separation, while those juveniles that had been carried less by fathers exhibited lower levels of maximum CORT in response to separation. In contrast, the regulation of the HPA axis, as assessed by the ability of a juvenile to return to baseline HPA function in the absence of a stressor, was influenced by differences in the quality of care provided by the mother. As shown in Figure 30.9(B), 6-month-old marmosets who received high levels of maternal grooming in the first month of life were more likely to have CORT levels that returned to baseline concentrations on the day

following the stressor, while those juveniles who received lower levels of maternal grooming had CORT levels that remained elevated on the day following the stressor. Thus, it is clear that although marmoset infants normally receive high quality and consistent care during early life, subtle differences in the amount of care received from potential caregivers in the family differential early care shapes both baseline HPA function (as seen earlier) and the dynamics of HPA responsiveness to stressors. We are currently monitoring stress reactivity and regulation at 12 months (subadult) and 18 months (adult) which will allow us to determine the persistence of these differential early care environments on later stress function.

## SUMMARY

Our understanding of social contributions to epigenesis is growing rapidly, particularly those aspects of development that are systematically influenced by variation in early maternal care. In this sense, variation in the nature of dyadic interactions between mothers and offspring can alter developmental trajectories in important ways. The data we've presented in this chapter provide, we believe, a compelling argument that family contexts, with the possibility of triadic and higher order social interactions, also constitute an important component of early epigenesis. The marmoset is an ideal animal model for evaluating these influences, since there are multiple classes of individuals providing care for offspring. Further, the ability to identify important sources of variation in care, and to track the consequences of these differences longitudinally, makes the marmoset particularly useful for providing insight into the ways in which family social environments shape offspring behavioral and physiological phenotypes.

## ACKNOWLEDGMENTS

Thanks go to Heather Jensen, Kim Patera, MaLinda Henry, and Denise Hightower for their dedicated service and high standards in maintaining the University of Nebraska at Omaha's Callitrichid Research Center from its inception in 1983. Michael Rukstalis contributed to the data and ideas presented in this chapter, and we thank Angie Burrell for access to her developing dataset on the consequences of variation in parental care in HPA function in marmosets. We gratefully acknowledge the long-standing support of the UNOmaha administration for our efforts in the science and conservation of callitrichid primates. This work presented in this chapter was supported by funds from the National Science Foundation (CRB 90-00094, IBN 92-09528, IBN 97-23842, IBN 00-91030) and the National Institutes of Health (HD 42882).

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