

Preparental Hormone Levels and Parenting Experience in Male Cotton-Top Tamarins, *Saguinus oedipus*

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Male cotton-top tamarins, *Saguinus oedipus*, display hormonal changes associated with parenting prior to the birth of their infants. Here we examined the hormonal changes that occurred in experienced and inexperienced fathers during the postconception period, prior to the birth of infants. Noninvasive techniques were used to collect urine from 10 male cotton-top tamarins (5 experienced and 5 inexperienced breeders) three times weekly during the 6-month gestation period. Samples were analyzed for prolactin, testosterone, dihydrotestosterone (DHT), and cortisol, averaged by gestational month. Experienced males showed elevated prolactin during the mate's 3rd gestational month, and the elevation correlated with the number of infants surviving from the previous birth (0, 1, and 2) but not with outcome of the current pregnancy. However, an experienced male with no infants present still showed elevated prolactin and some inexperienced males showed elevated prolactin just before parturition, suggesting noninfant cues are also important. While prolactin levels were influenced by the male's prior infant experience, testosterone levels did not differ between experienced and inexperienced males. Testosterone levels were significantly elevated for all males during the 3rd, 4th and 5th months but had no relationship with number of infants present or with outcome of current pregnancy. DHT decreased during the second half of pregnancy compared with testosterone but this finding was not consistent for every male. No significant changes occurred in cortisol levels. These results suggest that infant-rearing experience affected the hormonal responsivity of the male to his mate's current pregnancy. © 2000 Academic Press

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Males of biparental species may be involved in parenting behaviors immediately upon the birth of infants (Jones and Wynne-Edwards, 2000). Parental care can be seen even in males who are first-time fathers (Ziegler *et al.*, 1996; Jones and Wynne-Edwards, 2000). Therefore, it seems likely that prepartum physiological changes may be facilitating parenting behaviors in biparental males. Female mammals show many hormonal responses during pregnancy providing both the hormonal milieu for embryonic and fetal development and for facilitation of maternal behaviors (Bridges, 1996). Both physical and motivational changes prepare mothers for their role in infant care-taking (see Numan, 1994 for review). Whereas significant hormonal changes are known to occur in the female, little is known about hormonal changes in males during the prepartum period and how these hormonal changes may influence parenting behaviors.

Increased prolactin levels have been associated with parenting behavior in both males and females (Brown, 1993; Buntin, 1996; Dixson and George, 1982). Over 90% of birds show biparental care (Lack, 1968), and in many biparental species the male shows similar prolactin and behavioral changes as the female (for example, Goldsmith, 1982; Dawson and Goldsmith, 1985; Hiatt, Goldsmith, and Farner, 1987; Schoech, Mumme, and Wingfield, 1996). In the few species of rodents showing biparental behaviors, male hormonal changes vary across species. Male Mongolian gerbils, *Meriones unguiculatus*, have elevated levels of plasma prolactin throughout their mate's pregnancy and lactation period (Brown, Murdoch, Murphy, and Moger, 1995) while plasma prolactin levels in the biparental male California mouse, *Peromyscus californicus*, and the biparental male hamster *Phodopus campbelli*, are higher postpartum than when the female is pregnant (Guber-

nick and Nelson, 1989; Reburn and Wynne-Edwards, 1999). Androgen levels gradually increase throughout pregnancy for male Mongolian gerbils and hamsters but are lower during the postpartum period.

Different factors probably facilitate parental behavior in males and female mammals. In rodents, maternal behaviors are initiated by hormonal changes occurring within the pregnant female, whereas paternal behavior in rodents appears to be dependent on external cues such as mating, cohabitation with a pregnant mate, and pup stimuli (Brown *et al.*, 1995). These external cues may influence neuroendocrine changes that promote parental behavior. Parental care by male cotton-top tamarins, *Saguinus oedipus*, is essential to the survival of offspring in this species both in captivity and in the wild (Snowdon, 1996). Since the female usually gives birth to two large infants and is usually pregnant again within 2 to 4 weeks after birth, there is need for direct care of infants from another animal besides herself. Father tamarins begin carrying infants on the day of birth (Ziegler, Wegner, Carlson, Lazaro-Perea, and Snowdon, 2000).

Our previous studies on male cotton-top tamarins suggested that urinary prolactin levels are already elevated prior to the birth of infants and may indicate a prolactin response to external cues other than direct contact with infants (Ziegler, Wegner, and Snowdon, 1996; Ziegler, 2000; Ziegler *et al.*, 2000). Both experienced and inexperienced males showed higher levels of prolactin during the 2 weeks prior to infant birth than levels found in males living with nonpregnant females (Ziegler *et al.*, 1996). An inverse relationship between prolactin and testosterone has been reported for several species of birds and rodents (see Ziegler, 2000 for review; Reburn and Wynne-Edwards, 1999), but this relationship was not found in male tamarins during the first 2 weeks postpartum. Additionally, unlike the closely related common marmoset, *Callithrix jacchus* (Dixson and George, 1982; Mota and Sousa, 2000), male tamarins do not show a significant increase in prolactin following birth or any relationship between infant contact time and prolactin elevation (Ziegler *et al.*, 2000).

Our objectives were to assess whether hormonal changes occur prior to the birth of infants that may be involved in facilitating male infant care behaviors. Specifically, we measured levels of prolactin, testosterone, DHT, and cortisol in male tamarins from their mate's conception and throughout the gestation and the month following the birth. Since experience influences prolactin levels in males (Ziegler *et al.*, 1996), we wanted to determine if there were differences between

experienced and inexperienced males in their hormones prior to the birth of infants. Hormonal changes were also compared with respect to infant survival and male carrying effort as independent variable. Our goal is to provide insight into cues that facilitate male parental care in cotton-top tamarins.

MATERIALS AND METHODS

Subjects and Hormonal Sample Collection

Ten male cotton-top tamarins were studied from conception through their mate's pregnancy and during the postpartum period. The male tamarins lived either in large family cages ($3.0 \times 1.8 \times 2.3$ m) where they were the dominant and only breeding male or in pair cages ($1.5 \times 0.85 \times 2.3$ m) with their mate and any offspring. The tamarins were maintained on a 12-h day/night cycle and temperatures remained near 26°C. Routine colony maintenance and diet has recently been described for this colony (Ginther, Ziegler, and Snowdon, 2000).

For analysis of hormonal data, males were divided into the categories of experienced or inexperienced breeders according to whether they had previous experience raising their own infants. Having raised at least one set of his own infants qualified a male as experienced. All of the experienced and inexperienced males had younger siblings born at least twice while they were in the natal cage and therefore had comparable developmental experience with infants. Age of experienced males ranged from 4 to 7.5 years and all these males had been paired for 2 to 4 years prior to this pregnancy. Inexperienced males were from 2 to 3 years old and conception occurred from immediately after pairing to up to 8 months after pairing.

Urine samples were collected three times per week from each male at first morning void. Lights were turned on between 8 to 9 A.M. each morning and the collector would enter the cage. As the males urinated into a hand-held bucket, they were rewarded with a raisin. Each sample was mixed within the bucket, aliquoted into several tubes and centrifuged to remove any debris from the urine. Samples were stored frozen at -20°C until hormonal analyses. To protect the proteins during freezing, several aliquots were stored with the addition of 0.52 M glycerol.

Hormonal Analyses

All urine samples were analyzed for prolactin, testosterone, DHT, cortisol, and creatinine. Creatinine

TABLE 1
Hormonal Peaks in Male Cotton-Top Tamarin Urine during the Female's Pregnancy and Offspring Survival Prior to the Pregnancy and Following the Pregnancy

	Previous survival ^a	Gestational month of peak prolactin	Gestational month of peak testosterone	Outcome survival ^b	Percent carry ^c
Experienced males					
DI	0	4	5	1	79
NI	1	3	5	0	—
YE	1	3	6	1	83
TI	2	2	3	1	83
NK	2	2	5	2	84
Inexperienced males					
LN	No births	None	3	0	—
SQ	No births	6	4	0	—
YE	No births	5	6	1	79
WO	No births	6	6	1	52
JU	No births	None	3	2	67

^a Number of infants surviving from previous birth regardless of age of those infants.

^b Number of infants surviving from female's pregnancy.

^c Percentage of possible times males were carrying infants during the first 5 days postpartum.

was measured to correct for fluid variability between urine samples. Each steroid was divided by creatinine and expressed per milligrams of creatinine (mg/Cr). Details of the creatinine assay have been described (Ziegler, Scheffler, and Snowdon, 1995).

All assays used have been described and validated elsewhere. The urinary prolactin assay and its modifications have been described (Ziegler *et al.*, 1996, 2000). Our assay uses 1.5 ml of tamarin urine in duplicate concentrated to 50 μ l. The mean intraassay coefficient of variation (cv) for a tamarin pool was 7.10% and the interassay coefficient of variation was 19.23% ($n = 16$). Urinary testosterone and DHT have been shown to reflect gonadal function in the cotton-top tamarin (Ziegler, Carlson, Ginther, and Snowdon, 2000). Methods for separation by celite column chromatography and enzyme immunoassay (EIA) of testosterone and DHT have been reported (Ziegler *et al.*, 2000). Tritiated-labeled recoveries through solvolysis and celite chromatography were 89.39% ($n = 12$) for testosterone and 77.40% ($n = 12$) for DHT. Mean intra- and interassay CVs for testosterone were 3.47 and 18.06%, respectively, and for DHT were 3.39 and 20.23%, respectively. Methods for direct EIA measurement of cortisol in tamarin urine have been reported (Ziegler *et al.*, 1995). Mean intraassay coefficients of variation were 1.03 and 1.57% for the low and high pool and interassay coefficients of variation were 5.52 and 13.2%, respectively ($n = 16$).

Infant Data

Several methods were used to determine male-infant interactions and the results are shown in Table 1. For the experienced males, we recorded the number of surviving infants from the previous birth who were available for interaction with the father during the 6-month hormonal collection. The outcome of the current pregnancy was also recorded for all males by how many infants survived. The carrying data were derived from instantaneous scan samples which recorded the identity of the tamarin carrying the infants at five different times per day. A more detailed description of the method and validation is described in Ziegler *et al.* (2000). These data indicate the percentage of scan samples the males were observed carrying infants during the first 5 days.

Statistical Analyses

Gestational length was taken as 184 days since cotton-top tamarin females have a very reliable gestation length of 184 ± 1.14 days (6 months) in captivity (Ziegler, Bridson, Snowdon, and Eman, 1987). The last day of gestation was considered to be the day before birth. For each male, three samples per week were analyzed for hormone concentration during the 26-week pregnancy of the mate. All samples were analyzed for each hormone and averaged for each month of pregnancy. The last month of pregnancy was con-

sidered month 6 and the 1st month of pregnancy began at conception. For some analyses, urine samples collected and assayed for hormone concentration during the month following birth were also used. All hormonal data were converted to percentage of change in hormone levels by determining the level of change each month relative to the 1st month of the gestation. The month with the highest elevation was determined to be statistically different from the other months by determining the Z score for each male. Since the data did not have a normal distribution, we used nonparametric statistical analyses. Between-condition comparisons were made with Mann-Whitney U tests, and the Wilcoxon Signed Ranks Test was used to compare between months within a condition or for all males. The number of infants that survived the previous birth prior to the male's hormonal collection and the number of infants that survived as the outcome of the mate's pregnancy were correlated with the month of elevated levels of prolactin and testosterone during the pregnancy by Pearson product-moment correlation. P values <0.05 were considered significant.

RESULTS

Prepartum Prolactin Levels, Experience, and Infant Survival

We divided the males into experienced and inexperienced breeding males by whether they had previously reared infants. The experienced males had significantly higher mean prolactin levels than inexperienced males during the mate's pregnancy [$U = 49(7,7)$, $P = 0.002$]. Prolactin levels are influenced by the level of experience a tamarin male has had with previous births, but apparently not by age (Ziegler *et al.*, 1996, 2000), and this in turn influences the baseline prolactin levels for each male, therefore we changed the prolactin concentration for each month to percentage of change from month 1. All experienced males showed a significant increase in prolactin by the 3rd month of their mate's gestation (Fig. 1A). Calculating the Z scores, using a one-tailed test, the distribution of all peak months was significantly above the mean (Z scores ranged from 1.79 to 2.36). For two males, the highest prolactin increase occurred during the 2nd month, for two males the highest increase occurred during the 3rd month, and for one male the highest increase occurred during the 4th month (see Table 1). Prolactin levels in experi-

enced males were significantly increased during month 3 compared to month 1 ($Z = 2.03$, $n = 5$, $P = 0.04$), month 5 ($Z = 2.02$, $n = 5$, $P = 0.04$), month 6 ($Z = 2.02$, $n = 5$, $P = 0.04$), and postpartum ($Z = 2.02$, $n = 5$, $P = 0.04$) and a marginally significant difference was found between months 3 and 4 ($Z = 1.75$, $n = 5$, $P = 0.08$). For the inexperienced males, three of five males (60%) showed increases in prolactin in the last 2 months of pregnancy (months 5 and 6). While individual males showed changes by month, there were no significant increases for the inexperienced males ($Z = 0.67$ – 1.83 for months 2–6, P 's > 0.07 – 0.5).

For experienced males, the time in months to elevated prolactin correlated exactly with the number of surviving infants from the previous birth ($r = 1.00$, $y = -1.00x + 4.0$, $n = 5$). The more surviving infants, the sooner the prolactin elevation occurred during the gestational months (Table 1). However, every male showed an elevation in prolactin regardless of whether any infants survived. For one male, YE, the previous birth was 5 months prior to when conception would have occurred for the current pregnancy and therefore his infant would not have been dependent. We found no relationship between the timing of elevated prolactin levels and the outcome of the current pregnancy. Additionally, there was no relationship between the amount of time males carried infants and previous changes in prolactin levels in males during the mate's pregnancy. However, experienced males carried infants during the first 5 days postpartum significantly more than inexperienced males [$U = 11.5(4, 3)$, $P = 0.05$]. All breeding males carried the infants the majority of the scans during the first 5 days regardless of how many other helpers were present in the family.

Prepartum Testosterone, DHT, and Cortisol in Experienced and Inexperienced Males

For the experienced males prolactin levels showed the most change during first half of gestation while testosterone levels gradually increased throughout pregnancy, reaching highest elevation during the 4th and 5th months (Fig. 1B). Testosterone changes over the gestation were similar for inexperienced males. Experienced males did not differ significantly from inexperienced males for any month [U 's $> 8.0(5, 5)$, P 's > 0.25] and therefore we combined experienced and inexperienced males for further analyses.

Combined changes in testosterone over the gestation period were at their lowest during the 1st month

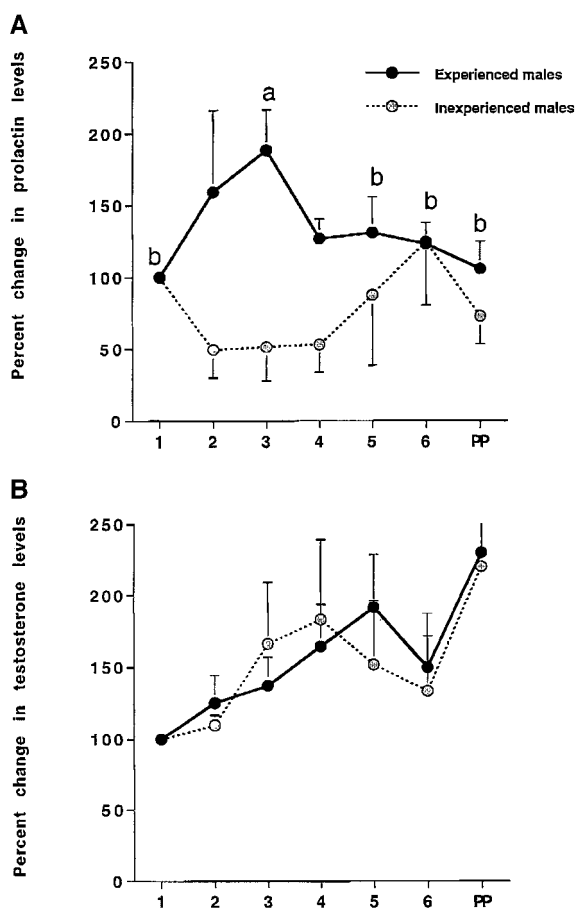


FIG. 1. Mean \pm SEM percentage changes in urinary prolactin and testosterone levels for five experienced and five inexperienced males during their mate's 6-month gestation and 1 month postpartum. Month 1 indicates the month following conception and PP indicates the month following the birth of the infants. $N = 5$ for all months except months 2 and 3 for the inexperienced males ($N = 4$). (A) Changes in prolactin levels for experienced males for each month where month 3 (a) was significantly higher than months 1, 5, 6, and PP (b), respectively, and near significant differences between months 3 and 4. For inexperienced males, none of the months were significantly different from each other. (B) Testosterone changes for all males showed the same pattern. Samples sizes were $N = 5$ for all months for experienced males and $N = 5$ for all months for inexperienced males except for months 2 and 3 ($N = 4$).

of the gestation and increased every month thereafter with highest levels occurring in months 4 and 5 (Fig. 2A). Levels dropped during month 6. Months 3, 4, and 5 were significantly higher than month 1 (month 3: $Z = 2.07$, $n = 9$, $P = 0.04$; month 4: $Z = 2.09$, $n = 10$, $P = 0.04$; month 5: $Z = 2.19$, $n = 10$, $P = 0.03$) and months 3 and 5 were significantly higher than the month 2 (month 3: $Z = 1.96$, $n = 9$, $P = 0.05$; month 5: $Z = 1.96$, $n = 10$, $P = 0.05$). Unlike prolactin, the month of highest elevation of testosterone did not

correlate with the number of infants surviving from the previous birth nor with the outcome of the present birth (Table 1; r 's = -0.49 for previous birth and 0.42 for the outcome birth).

Testosterone and DHT had similar patterns of change during the first half of pregnancy when prolactin levels were elevated but mean DHT levels dropped during the second half of gestation (Fig. 2A).

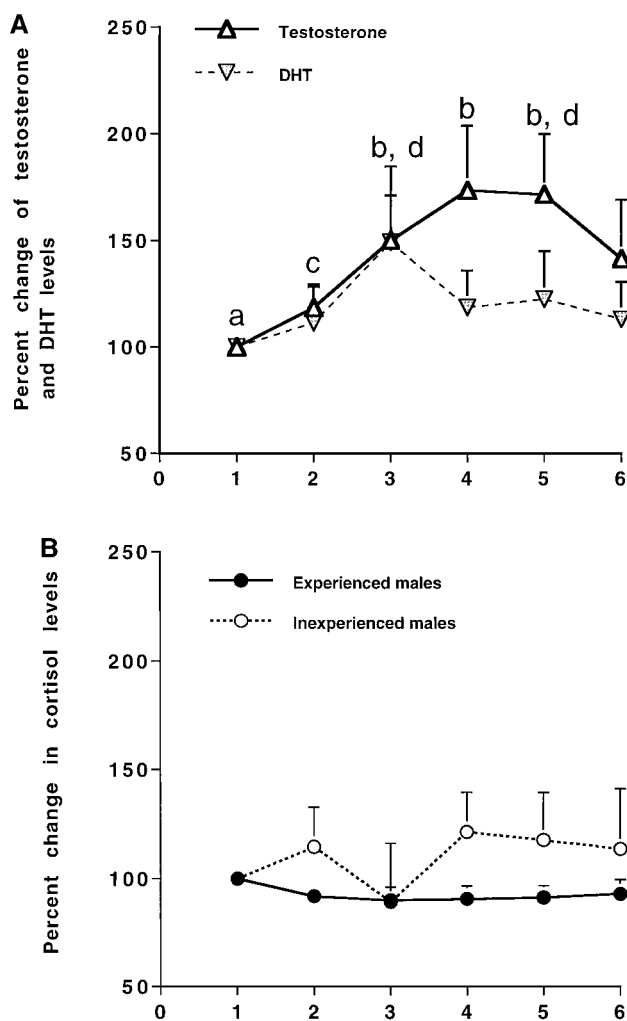


FIG. 2. (A) Mean \pm SEM percentage change of testosterone and DHT in all male cotton-top tamarins across the 6 gestational months. For testosterone, month 1 (a) was significantly different than months 3, 4, and 5 (b) and month 2 (c) was significantly different from months 3 and 5. No significant differences were found by month for DHT. $N = 10$ for all months except months 2 and 3 ($N = 9$). (B) Mean \pm SEM urinary cortisol levels for experienced and inexperienced male cotton-top tamarins during their mate's 6-month gestation and postpartum period (PP). $N = 5$ for all months except for months 2 and 3 for the inexperienced males ($N = 4$).

No significant changes in DHT occurred between the gestational months for all males together (Z 's = 0.28–1.01, P 's > 0.31–0.86) or for experienced or inexperienced males analyzed separately (experienced: Z 's = 0.14–1.75, P 's > 0.08–0.89; inexperienced: Z 's = 0.37–1.21, P 's > 0.23–0.71).

Cortisol levels changed little throughout pregnancy (Fig. 2B). Significant changes for cortisol were not observed for either the experienced males (Z 's = 0.14–1.48; P 's > 0.14–0.89) or the inexperienced males (Z 's = 0.37–1.46; P 's > 0.14–0.72).

DISCUSSION

Significance of Prepartum Prolactin in Male Tamarins

Significant changes in prolactin levels occurred well before infant birth in male cotton-top tamarins. Based on the hormonal profiles shown in this study, experienced but not inexperienced breeding male cotton-top tamarins showed significant changes in prolactin levels during their mate's pregnancy but prior to the birth of infants, reaching their highest levels with a mean of the 3rd gestational month. Only 60% of the inexperienced males showed any increase in prolactin levels, however, and these changes occurred during the 5th and 6th months. The lack of consistent changes in prolactin in inexperienced male cotton-top tamarins suggests that prolactin changes are modulated by experiential factors occurring after the males became breeders. Our previous work has shown that prolactin levels are related to experience in infant care with higher levels of prolactin occurring in the most experienced males (Ziegler *et al.*, 1996, 2000). The present data provide evidence that direct infant-rearing experience alters the hormonal responsiveness of the male during his mate's current pregnancy.

Each of the males in the present study, whether experienced or inexperienced breeders, have had prior experience with infants while living with their natal family. Several studies have indicated that both male and female cotton-top tamarins have little success in rearing infants if they have not had exposure to their younger sibling's births during prepubertal development (Snowdon, 1996; Tardif, Richter, and Carson, 1984; Johnson, Petto, and Sehgal, 1991). There is some evidence that prolactin levels may also be elevated in young adults living in the family group while participating in carrying younger siblings (Ziegler *et al.*,

1996; Mota and Sousa, 2000). But prolactin levels are low in males housed in pairs without infants (Ziegler *et al.*, 1996). Since males do not show good parenting behaviors if they have not had exposure during their development, then the early experience with infants may have an effect on the prolactin system. Whether this effect initiates an onset of parenting behaviors or whether the prolactin fluctuations influence the quality of care is unknown.

Several factors may influence the changes in prolactin for experienced breeding males. The perfect correlation between the timing of the peak levels of prolactin by month and the number of surviving infants provides evidence that part of the prolactin increase may be in response to interactions with the previous infants who are generally around 2 to 3 months of age. This is the age at which infants are being weaned and learning to eat solid food. Male cotton-top tamarins are actively involved in the weaning process in our colony by distracting the infants and sharing food (Roush and Snowdon, in press). However, males whose infants died or had infants weaned 2 or 3 months before their mate's pregnancy still showed elevated prolactin levels, suggesting that infant interactions alone do not account for all of the prolactin response. Only experienced males showed the peak increase in prolactin during the first half of the gestation, suggesting that interacting with infants may influence prolactin changes. On the other hand, prolactin levels peaked even for the experienced male whose previous infants had not survived, DI. Also, the previous birth of one of the experienced males, YE, was actually 5 months prior to the changes in prolactin, unlike the other males where the infants were only 2 to 3 months of age. These two findings suggest that cues other than interactions with previous infants contribute to the prolactin changes. Males may be receiving cues from their mates to promote hormonal changes and thereby influencing parental behavior prior to the birth similarly to some rodents (Brown *et al.*, 1995). Although the elevated prolactin levels during the infant's gestation were not sustained, the hormonal increase may raise baseline levels of prolactin, which increases with the level of experience by previous births (Ziegler *et al.*, 1996, 2000). To determine whether the prolactin elevation we found in cotton-top tamarin males is due to infant stimuli or to other cues that occur during the female's pregnancy, we would need to examine males who are interacting with infants without an ensuing pregnancy. Additionally, if males who lose both their infants still show the prolactin peak during their female's next pregnancy, it

suggests that the cues promoting prolactin elevation are not only from infant stimuli and may come from the pregnant female.

In callitrichids, increased prolactin levels are correlated with increased infant contact (Dixon and George, 1982) and increased parental experience (Ziegler *et al.*, 1996). Inexperienced common marmosets showed increased levels of prolactin after infant retrieval (Roberts, Jenkins, Lawler, Wegner, Norcross, Bernhards, and Newman, submitted) and a decrease in infant retrieval after administration of bromocriptine to lower prolactin (Roberts, Jenkins, Lawler, Wegner, and Newman, submitted). These studies suggest that prolactin increase is directly responsive to infant stimuli and that increased prolactin levels increase parenting behaviors or respond to parenting behavior.

In contrast to common marmosets and related species where females do most of the infant care in the 1st week (Tardif, 1996; Nunes, Fite, and French, 2000), male cotton-top tamarins show direct involvement with neonates and carry them at least as much as females in the first 5 days (this article; Ziegler *et al.*, 2000). Thus, if hormonal changes in male cotton-top tamarins do promote infant interactions, then they must occur prior to infant birth to ensure immediate care for the neonates by the father. This is seen in many biparental birds where males show elevated prolactin during the egg incubation (for example, king penguins: Garcia, Jouventin, and Mauget, 1996). Additionally, male tamarins are also pair-bonded with their cohabiting female (Porter, 1994). If the male is receiving cues promoting hormonal changes from the female, then the question becomes how are the cues emitted and how are they received?

Cues could be olfactory, direct male–female contact, or hormonal changes within the female. Olfactory stimuli could arise from the female. Male tamarins have well-developed vomeronasal organs (Wysocki, 1979) while female tamarins have well-developed scent glands and spend considerable time scent marking their environment (Epple, 1986; Savage, Ziegler, and Snowdon, 1988). Chemical signals received via the vomeronasal organ or the accessory olfactory epithelium have direct pathways to the areas of the brain concerned with reproduction and behavior. An intact vomeronasal organ is required for reception of many priming pheromones (Vandenbergh, 1994). Alternatively, after conception females may increase their contact time with males to ensure that males will be available for parenting when the infants are born. This direct increase in contact may stimulate certain hormones such as oxytocin and vasopressin (Uvnas-

Moberg, 1997). These hormones appear to be important in parental behaviors in certain rodents. Increased oxytocin inhibits infanticide in house mice (McCarthy, 1990) and facilitates pair-bonding in voles (Williams, Insel, Harbaugh, and Carter, 1994). Pair-bonding may activate neural circuits involved in rodent paternal behavior (Brown *et al.*, 1995). Pair-bonding in cotton-top tamarins may also exert physiological influences on parenting; however, no data exist. Hormonal changes in female primates might also produce modulatory effects on the male (Jacob and McClintock, 2000; Ziegler *et al.*, 2000).

Elevated Prepartum Testosterone and Parenting Behaviors

While only experienced males showed an increase in prolactin levels during early pregnancy, all males showed a significant increase in testosterone levels during the 3rd, 4th, and 5th months. Testosterone changes appear to be independent of experience prior to birth. We did not find an inverse relationship between testosterone and prolactin levels during the postpartum period in father tamarins (this article; Ziegler *et al.*, 2000). All of the males, both experienced and inexperienced, showed elevated prolactin and testosterone at different times during the gestational period. Some species of biparental rodents have shown a reciprocal relationship with testosterone and prolactin, and for these species, testosterone levels fall at parturition (Brown, Murdoch, Murphy, and Moger, 1995; Reburn and Wynne-Edwards, 1999). Testosterone levels are normally lower during the parenting period than during the breeding period and may be even lower in nonparenting males. Lower testosterone is thought to suppress infanticidal aggression (Reburn and Wynne-Edwards, 1999). Prolactin and testosterone elevations do not occur at the same time in cotton-top tamarins during the mate's pregnancy, and it does not appear that these hormones are interdependent upon one another during the preparenting period.

Increased testosterone in the male during the second half of the gestation may be associated with increased mate guarding or territorial defense. Male monogamous mating systems are not only associated with pair-bonding but also with increased aggression toward strangers for defense of territory and mate (Kleiman, 1977; Clutton-Brock, 1989). Male monogamous hamsters show increased levels of testosterone as birth approaches and an increase in mate guarding (Wynne-Edwards and Lisk, 1988). Cotton-top tamarins are known to be highly aggressive to intruders in

captivity (French and Snowdon, 1981; Harrison & Tardif, 1988) and are especially responsive to mate guarding when the female is pregnant (Porter, 1994). They form strong pair relationships quickly after pairing which are maintained even after separation and association with novel tamarins of the opposite sex (Porter, 1994). Strong pair relations are probably necessary for successful infant care by both parents.

We were surprised at the divergence in testosterone and DHT levels during gestation. Sixty percent of the males (6/10) showed different patterns of testosterone and DHT excretion during the second half of the mate's pregnancy while for the other 40%, testosterone and DHT followed similar patterns. Whether the differences between DHT and testosterone are due to differential metabolism of testosterone into DHT and other steroids is unknown.

Parenting Experience and Cortisol Response

The lack of change in cortisol throughout the gestational period for inexperienced males was surprising. In our colony, cortisol levels increase significantly at the time a tamarin is removed from the natal family and paired (Ziegler *et al.*, 1995; Ginther *et al.*, 2000). In females, cortisol levels return to normal baseline levels as soon as they conceive but are significantly elevated during the last half of pregnancy. Here we found that cortisol levels in inexperienced males did not decline during the entire first pregnancy and postpartum period. Interestingly, two of the inexperienced males had cortisol levels within the range of experienced males, and both of these males lost their infants following birth (see LN and SQ, Table 1).

In species where male paternal care has evolved, males are an important component to the survival of the offspring (Emlen, 1991; Koenig, Pitelka, Carmen, Mumme, and Stanback, 1992). As with the cotton-top tamarin, in biparental (or cooperatively breeding) species males are required to assist in all aspects of infant rearing except the actual lactation and early feeding. Therefore, males need to be as ready for their role as do females. Experience appears to play an important part in a male's hormonal response and it is possible that the parenting experience itself sensitizes the male hormonal system in a similar manner to how pup exposure sensitizes virgin female rates (Bridges, 1996). Heightened hormonal responses elicited during the mate's gestation may contribute to the overall success of a male in helping to rear infants.

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