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Elevated urinary testosterone excretion and decreased maternal caregiving effort in marmosets when conception occurs during the period of infant dependence

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Abstract

The proximate mechanisms that regulate transitions in mammalian female reproductive effort have not been widely studied. However, variation in circulating levels of the androgenic steroid hormone testosterone (T) appears to mediate a trade-off between investment in current and future offspring in males [Ketterson, E.D., Nolan, V., Jr., 1994. Hormones and life histories: an integrative approach. In: L.A. Real (Ed.), Behavioral Mechanisms in Evolutionary Ecology, University of Chicago Press, Chicago, pp. 327–353; Ketterson, E. D., Nolan, V., Jr., 1999. Adaptation, exaptation, and constraint: A hormonal perspective. *Am. Nat.* 154S, S4–S25]. The purpose of this study was to investigate the possibility that T is also associated with transitions in the reproductive effort of females, by examining the relationship between urinary T excretion, maternal caregiving behavior, and the timing of the postpartum conception in female Wied's black tufted-ear marmosets (*Callithrix kuhlii*). We examined the maternal carrying effort and peripartum T profiles of six females across two conditions: (1) when they conceived during the period of infant dependence (DPID), such that gestation was coupled with lactation; and (2) when the same females conceived after the period of infant dependence (APID). We also assessed the relationship between postpartum T levels and caregiving effort. When female marmosets conceived DPID, they dramatically reduced their caregiving effort, and had higher levels of urinary T, relative to when they conceived APID. Further, the litter-to-litter changes in maternal caregiving effort that we observed were related to variation in urinary T excretion; as weekly levels of urinary T excretion increased, concurrent caregiving effort declined. Our results suggest that variation in T secretion may regulate transitions in female reproductive behavior, and that the regulation of male and female parental behavior may be mediated by homologous neuroendocrine mechanisms.

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Introduction

Decades of research on the behavioral ecology of mammalian maternal care have demonstrated that females are anything but indiscriminate about the care they provide

to their young. When they have difficulty meeting their own subsistence needs, and when their physical condition is poor, females may invest less in their current offspring's fitness in lieu of maintaining or improving maternal condition and the possibility of producing future offspring (e.g., Clutton-Brock, 1991; Hrdy, 1999; Lee et al., 1991). It appears, therefore, that the quality and quantity of care that mothers provide to any given offspring is the result of complex trade-offs between their ability to invest in current

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45 offspring and the probability of producing offspring in the
46 future (Trivers, 1974).

47 The proximate mechanisms that regulate transitions in
48 mammalian female reproductive effort—toward preparation
49 for and production of future offspring, and away from the
50 rearing of current offspring—have not been widely studied.
51 However, variation in circulating levels of the androgenic
52 steroid hormone testosterone (T) appears to mediate a trade-
53 off between investment in current and future offspring in
54 males (Ketterson and Nolan, 1994, 1999). For example,
55 male dark-eyed juncos (*Junco hyemalis*) with experimen-
56 tally elevated T spent less time provisioning and defending
57 nestlings but spent more time singing, maintaining their
58 territories, and obtaining extra-pair fertilizations, than
59 controls (e.g., Cawthorn et al., 1998; Chandler et al.,
60 1994; Hegner and Wingfield, 1987; Ketterson and Nolan,
61 1992; Raouf et al., 1997). Male house finches (*Carpodacus*
62 *mexicanus*) treated with exogenous T sang at a higher rate,
63 but fed their nestlings at a lower rate (Stoehr and Hill,
64 2000). Clark and his colleagues reported that male
65 Mongolian gerbils (*Meriones unguiculatus*) positioned
66 between two males in utero (2M males) not only had higher
67 circulating levels of T in adulthood (Clark et al., 1992b), but
68 that they also spent less time in contact with pups (Clark et
69 al., 1997) and were more successful at impregnating females
70 (Clark et al., 1992a) than males positioned between two
71 females (2F males). In contrast, 2F males engaged in less
72 sexual behavior than 2M males, but spent more time in
73 contact with pups, even when their mates were away from
74 the nest (Clark et al., 1997). Variation in circulating levels of
75 T is also associated with variation in the reproductive effort
76 of individual males. For instance, decreases in T are known
77 to accompany the onset of paternal care in fish (e.g.,
78 bluegill, *Lepomis macrochirus*: Kindler et al., 1991; plainfin
79 midshipman, *Porichthys notatus*: Knapp et al., 1999; black-
80 chinned tilapia, *Sarotherodon melanotheron*: Specker and
81 Kishida, 2000), birds (e.g., red-cockaded woodpecker,
82 *Picoides borealis*: Khan et al., 2001; white-crowned
83 sparrow, *Zonotrichia leucophrys pugetensis*: Wingfield
84 and Farner, 1978; song sparrow, *Melospiza melodia*:
85 Wingfield and Goldsmith, 1990), rodents (e.g., Mongolian
86 gerbil: Brown et al., 1995; Djungarian hamster, *Phodopus*
87 *campbelli*: Reburn and Wynne-Edwards, 1999; but also see
88 Trainor and Marler, 2001, 2002), and primates (e.g., Wied's
89 black tufted-ear marmoset, *Callithrix kuhlii*: Nunes et al.,
90 2000; human: Berg and Wynne-Edwards, 2001; Fleming,
91 2002; Storey et al., 2000). To the degree that male and
92 female parental behaviors appear to be regulated by
93 common neuroendocrinological mechanisms (e.g., Kelley,
94 1988; Rosenblatt and Ceus, 1998; Wynne-Edwards, 2001;
95 Wynne-Edwards and Reburn, 2000), it seems likely that T
96 might also facilitate trade-offs between investment in
97 current versus future offspring in females.

98 In fact, there are reports that maternal caregiving
99 behavior is, at least to some extent, androgen-dependent.
100 Pre- and perinatal exposure to androgens, for instance, has

101 been shown to profoundly influence parental effort in
102 adulthood. Female rats (*Rattus norvegicus*) treated with
103 testosterone propionate in utero, for example, showed
104 suppressed responsiveness to pups in adulthood (Ichikawa
105 and Fujii, 1982; Juárez et al., 1998; Quadagno and Rock-
106 well, 1972; but also see Lonstein et al., 2002; Stern and
107 Strait, 1983). Additionally, there are numerous reports that T
108 levels decrease with the onset of maternal care and/or
109 exposure to offspring (e.g., plainfin midshipman: Knapp et
110 al., 1999; domestic chicken, *Gallus domesticus*: Richard-
111 Yris et al., 1987; white-crowned sparrow: Wingfield and
112 Farner, 1978; rat: Bridges et al., 1982; rabbit, *Oryctolagus*
113 *cuniculus*: González-Mariscal, 2001; sheep, *Ovis aries*:
114 Strott et al., 1974; human: Fleming et al., 1997). Taken
115 together, these studies provide some evidence, albeit
116 preliminary, to suggest that T inhibits parental effort in
117 females, as it does in males.

118 Primates belonging to the New World family Callitrichi-
119 dae, the marmosets and tamarins, are characterized by
120 distinctive reproductive traits that make them ideally suited
121 for investigations into the proximate mechanisms that
122 regulate maternal trade-offs between future and current
123 offspring. A postpartum ovulation occurs 2–4 weeks
124 following birth (French et al., 1996; Ziegler et al., 1990)
125 so that females can conceive while nursing, carrying, and
126 otherwise caring for their current litter of (typically) twin
127 infants, which at birth can weigh as much as 15–25% of the
128 female's own body weight (Kleiman, 1977). In every
129 species studied to date, females share the responsibility of
130 infant care with members of their family or social group
131 (e.g., Cleveland and Snowdon, 1984; Goldizen, 1987;
132 Snowdon, 1996). However, we recently reported that the
133 degree to which individual female marmosets relinquished
134 the responsibility of infant care to others varied from litter to
135 litter and depended, at least in part, on the timing of the
136 postpartum conception (Fite et al., submitted for publica-
137 tion). When females conceived after the period of infant
138 dependence (APID), at which time their current litters had
139 begun independent locomotion and feeding, they only
140 gradually reduced the amount of time they spent carrying
141 their current litters over subsequent weeks. Yet, when the
142 same females conceived during the period of infant
143 dependence (DPID), during which time females face the
144 energetic challenge of nursing infants every few hours and,
145 along with other group members, carrying infants almost
146 constantly, they exhibited an abrupt and significant decrease
147 in the amount of time that they spent carrying their current
148 litters—a decrease that occurred when infants were only 2
149 weeks of age. It seems likely then that callitrichid females
150 are equipped with the ability to make trade-offs between
151 current and future offspring when energetic demands are
152 increased—when gestation was coupled with lactation, the
153 female marmosets in our study appeared to have exhibited a
154 shift of investment away from their current litters and
155 toward developing fetuses. In light of reports that female
156 primates exhibit increases in maternal serum androgens

157 early in gestation (see review in [Castracane et al., 1998](#)), it
158 also seems likely that T could have mediated the redirection
159 of female reproductive effort.

160 The purpose of this study was to investigate the
161 possibility that T is associated with transitions in the
162 reproductive effort of individual females, by examining
163 the relationship between urinary T excretion, maternal
164 caregiving behavior, and the timing of the postpartum
165 conception in female Wied's black tufted-ear marmosets (*C.*
166 *kuhlii*). Previous studies have associated transitory variation
167 in urinary levels of T with transitory shifts in the
168 reproductive effort of *C. kuhlii* males. In fact, decreased
169 urinary T excretion was found to correspond with the
170 postpartum shift from mating effort to parental effort ([Nunes
171 et al., 2000, 2001](#)). Therefore, we hypothesized that if T
172 mediates a trade-off between current and future offspring in
173 females, and if female marmosets shift investment away
174 from their current litters and toward developing fetuses
175 when conception occurs DPID ([Fite et al., submitted for
176 publication](#)), then females should have higher peripartum
177 levels of T and exhibit less maternal caregiving effort when
178 conception occurs DPID versus APID. Additionally, we
179 examined the relationship between postpartum urinary T
180 levels and infant-carrying effort, to determine whether
181 observed changes in maternal investment were associated
182 with variation in T excretion.

183 Methods

184 *Subjects and housing*

185 The subjects of this study were adult female Wied's black
186 tufted-ear marmosets, and their families, housed at the
187 University of Nebraska at Omaha's Callitrichid Research
188 Center. Marmosets were housed in wire mesh cages (1.6 ×
189 0.9 × 2.4 m), which were furnished with natural branches, a
190 feeding platform, a nest box, and an assortment of enrich-
191 ment devices. A 12 h/12 h light/dark cycle was controlled
192 by automatic timers, with light onset occurring at 0800 h.
193 Neighboring family groups were always at least 1 m apart
194 and were denied visual, but not auditory or olfactory,
195 contact. Our routine husbandry practices were designed to
196 minimize disturbance to the normal day-to-day activities of
197 the animals. We limited marmosets' exposure to unfamiliar
198 humans as much as possible, and we handled the animals
199 only when it was necessary to administer veterinary care.
200 For further details of animal housing and husbandry, see
201 [Schaffner et al. \(1995\)](#).

202 The selection criterion for individuals to include in this
203 study was the timing of females' postpartum conception. We
204 identified adult females ($N = 6$) who gave birth to full-term,
205 surviving litters followed by conception DPID and, at a
206 separate reproductive attempt, APID. When more than one
207 DPID or APID conception occurred for a female, we
208 randomly selected one conception per female. To distin-

209 guish between DPID and APID conditions, we referred to
210 [Tardif et al.'s \(1998\)](#) chronology of early marmoset
211 development, which emphasized weekly changes in the
212 degree to which infants rely on caregivers for nutrition and
213 transport. We operationally defined conception DPID as
214 conception during the first 3 weeks postpartum, because
215 infants exhibit little, if any, independent feeding or
216 locomotion during this time (common marmoset, *C.*
217 *jacchus*: [Tardif et al., 2001](#)). During this phase of develop-
218 ment, females nurse their infants every few hours (common
219 marmoset: [Missler et al., 1992](#)) and, along with other group
220 members, carry infants more than 90% of the time (common
221 marmoset; cotton-top tamarin; golden lion tamarin, *Leonto-
222 pithecus rosalia*; saddle-back tamarin, *S. fuscicollis*; silvery
223 marmoset, *C. argentata*; see review in [Tardif et al., 1993](#)).
224 This care is energetically costly for females; lactation is the
225 most energetically expensive component of reproduction for
226 female mammals (see review in [Gittleman and Thompson,
227 1988](#)), and infant carrying comes at a 21% increase in the
228 caloric cost of traveling ([Tardif, 1996](#)). We operationally
229 defined conception APID as conception occurring 4 weeks
230 following birth, and later. Weeks 4–6 postpartum are a
231 transitional period for marmoset infants. During this time
232 period, males replace females as the primary caregiver
233 (Wied's black tufted-ear marmoset: [Fite et al., submitted for
234 publication; Nunes et al., 2000](#)), and infant locomotion and
235 feeding becomes increasingly independent (common mar-
236 moset: [Tardif et al., 1998](#)). By weeks 7–10, infants exhibit
237 locomotion that is completely independent, as well as
238 independent feeding, although sporadic nursing bouts can
239 still occur.

240 [Table 1](#) presents demographic and reproductive data for
241 each female. Individual females did not differ significantly
242 in age between DPID and APID conditions ($t_5 = 0.57$, NS),
243 nor did their male partners ($t_5 = 0.56$, NS). Neither litter
244 sizes ($t_5 = 0.00$, NS) nor the number of alloparents present
245 to assist each female in the rearing of offspring ($t_5 = -0.42$,
246 NS) differed significantly between DPID and APID
247 conditions. Each of the females in this study had experience
248 caring for infants, prior to the commencement of this study;
249 all six females had extensive sibling-rearing experience as
250 alloparents, and three females (Bas, Jin, Pix) had experience
251 rearing their own offspring.

Behavioral measures

252
253 Observations of maternal carrying effort were conducted
254 between August 1996 and August 2001. Our observational
255 protocol employed the "all-occurrences" recording techni-
256 que ([Martin and Bateson, 1993](#)), using the Observer 3.0®
257 (Noldus Information Technology, Leesburg, VA, USA)
258 computerized behavioral recording program. Family groups
259 were observed for 20 min, five times per week, for the first 9
260 weeks of infant life (total observation time per litter, across
261 9 weeks = 15 h; total observation time for study = 180 h).
262 Observations were conducted at randomly selected times

Table 1
Demographic data for mothers when they conceived DPID and APID

Female ID	Timing of conception (postpartum week) ^a		Female age (year)		Male age (year)		Litter size		Number of alloparents	
	Conception DPID	Conception APID	Conception DPID	Conception APID	Conception DPID	Conception APID	Conception DPID	Conception APID	Conception DPID	Conception APID
t1.1	2	9	3.00	3.42	2.39	2.82	2	2	2	3
t1.2	2	4	7.33	6.91	12.97	12.55	2	1	2	1
t1.3	2	7	5.05	4.63	8.43	8.01	1	2	1	1
t1.4	2	6	4.48	3.56	4.58	3.66	1	2	1	2
t1.5	2	7	5.78	5.36	6.42	6.01	2	2	2	1
t1.6	2	6	2.11	2.96	5.74	6.58	2	1	2	3
t1.7	2.00 ± 0.00	6.50 ± 0.67	4.63 ± 0.77	4.47 ± 0.61	6.76 ± 1.49	6.61 ± 1.42	1.67 ± 0.21	1.67 ± 0.21	1.67 ± 0.21	1.83 ± 0.40
t1.8	^a Postpartum week during which conception occurred (i.e., conception during week 1 postpartum occurred 1–7 days postpartum, conception during week 2 postpartum occurred 8–14 days postpartum, etc.).									

between 0700 and 1800 h, but never occurred less than 1 h preceding, or subsequent to, the a.m. feeding. All behavioral observations were conducted by one individual (J.E.F.), with whom the animals were very familiar. The observer sat approximately 2 m from each cage, and began conducting a behavioral observation only after a 10-min habituation period. Mothers were determined to be carrying infants when one or more infants were observed clinging to the body or pelage of a parent or alloparent. We did not distinguish between the carrying of one versus two infants, because infants born into large social groups are not generally carried by the same individual (cotton-top tamarin: Price, 1990, 1992a,b), and there is evidence that there are few additional costs associated with carrying more than one infant at a time (e.g., Saddle-back tamarin: Goldizen, 1987; cotton-top tamarin: Price, 1992c).

Endocrine measures

Urine collection

Urine samples were collected two to five times per week from the six females in this study, as well as from other animals in our colony, as part of routine colony husbandry. A noninvasive, stress-free collection procedure previously described (French et al., 1996) was utilized. Urine samples were collected between 0600 and 0800 h, centrifuged at 7000 rpm for 2 min to remove detritus, and the supernatant was then transferred to a clean mini-vial for storage. All samples collected were catalogued and stored at –20°C until assayed.

Hormone assays

For each female, two urine samples per week were assayed for T and pregnanediol glucuronide (PdG) and their values averaged, providing a weekly estimate of urinary T and PdG excretion. Concentrations of T and PdG in peripartum urine samples were determined using enzyme immunoassays previously described and validated for use with *C. kuhlii* (T: Nunes et al., 2000; PdG: French et al., 1996). T was extracted from samples with diethyl ether before assays were performed. We measured hormone concentrations in 12 T assays and 12 PdG assays. Intra-assay coefficients of variation, determined from duplicate evaluations of pooled marmoset urine run within assays, were 5.37% and 6.91% for high concentration pools and 3.10% and 11.15% for low concentration pools in T and PdG assays, respectively. Inter-assay coefficients of variation, determined from evaluations of pooled marmoset urine run between assays, were 11.36% and 6.48% for high concentration pools and 13.74% and 17.87% for low concentration pools in T and PdG, respectively. All hormone concentrations were corrected for the creatinine concentration of each sample. Creatinine concentrations were measured by a modified Jaffé end-point assay (Tietz, 1976), which was previously described and validated for *C. kuhlii* (French et al., 1996).

316 Identification of postpartum conception

317 To determine the timing of females' postpartum con-
 318 ception, we monitored females' postpartum urinary PdG
 319 levels across the first 9 weeks of infant life. French et al.
 320 (1996) previously described patterns of urinary PdG
 321 excretion across the reproductive cycle in *C. kuhlii*, and
 322 we used these parameters to identify the postpartum week in
 323 which conception occurred. While there were individual
 324 differences in absolute urinary PdG concentrations, qual-
 325 itative changes in PdG profiles across the postpartum period
 326 were similar among females in each condition. The first
 327 postpartum ovulation occurred approximately 14 days
 328 postpartum (mean postpartum to ovulation interval: $13.6 \pm$
 329 1.2 days; French et al., 1996). For nonconceptive cycles,
 330 PdG levels returned to preovulatory follicular levels within
 331 25 days (mean duration in days from successive luteinizing
 332 hormone (LH) peaks: 24.9 ± 0.60 days; French et al., 1996).
 333 For conceptive cycles, there was a rapid elevation in urinary
 334 PdG excretion during the first 30 days of pregnancy, and
 335 PdG levels remained high for the first two trimesters of
 336 pregnancy (mean first trimester urinary PdG levels: $33.7 \pm$
 337 8.4 $\mu\text{g}/\text{mg}$ Cr; mean second trimester urinary PdG levels:
 338 39.0 ± 10.9 $\mu\text{g}/\text{mg}$ Cr; mean gestation length: 143.1 ± 1.6
 339 days; French et al., 1996). Therefore, the postpartum week
 340 during which females' PdG levels initially rose beyond
 341 preovulatory follicular levels was identified as the week of
 342 conception. The timing of each female's conception in DPID
 343 and APID conditions is presented in Table 1.

344 Statistical analyses

345 To compare levels of maternal investment in offspring
 346 when females conceived DPID versus APID, a 2-way
 347 completely within-subjects ANOVA (2×9 ; conception
 348 condition \times postpartum week) was conducted on infant
 349 carrying effort across the first 9 postpartum weeks. To
 350 compare patterns of androgen excretion when females
 351 conceived DPID versus APID, a 2-way completely within-
 352 subjects ANOVA (2×13 ; conception condition \times
 353 peripartum week) was conducted on urinary T concen-
 354 trations across the peripartum period—from week -4
 355 prepartum through week 9 postpartum. Post hoc analyses
 356 were conducted using the Tukey test (Keppel, 1991).
 357 Additionally, we used Pearson correlation coefficients to
 358 examine the relationship between T and maternal effort. An
 359 α level of 0.05 was adopted for all statistical tests, and all
 360 data are presented as $\bar{X} \pm \text{SEM}$.

361 Results

362 Maternal caregiving behavior and timing of conception

363 Maternal carrying effort was influenced by the timing of
 364 the postpartum conception. A significant interaction
 365 between conception condition and postpartum week [$F(8,$
 366 $40) = 2.43, P = 0.03$] indicated that the effect of conception

condition on infant carrying effort varied by postpartum 367
 week. As illustrated in Fig. 1, when females conceived 368
 DPID, their carrying effort at week 2 postpartum ($12.09 \pm$ 369
 3.38 min/hr) was significantly less than when they 370
 conceived APID (29.80 ± 8.39 min/h; $P < 0.05$). Individual 371
 carrying data, by female, are presented in Table 2. With the 372
 exception of one female (Bon: carrying in DPID condition = 373
 7.51 ± 4.29 min/h; carrying in APID condition = $7.31 \pm$ 374
 2.15 min/h), females spent less time carrying their infants 375
 when they conceived DPID than when they conceived 376
 APID. 377

Urinary testosterone excretion and timing of conception 378

Females' urinary T profiles (Fig. 2, top panel) were 379
 characterized by decreasing levels between week -4 380
 prepartum (473.05 ± 56.19 ng/mg Cr) and week 1 381
 postpartum (177.96 ± 18.11 ng/mg Cr), with the greatest 382
 week-to-week decrease (177.78 ± 31.48 ng/mg Cr) occur- 383
 ring between week -1 prepartum (355.74 ± 33.58 ng/mg 384
 Cr) and week 1 postpartum (177.96 ± 18.11 ng/mg Cr). T 385
 levels were lowest at week 1 postpartum (177.96 ± 18.11 386
 ng/mg Cr), and rose across the following 8 weeks. The 387
 greatest week-to-week increase (325.11 ± 115.94 ng/mg Cr) 388
 in T levels occurred between weeks 8 (502.82 ± 59.40 ng/ 389
 mg Cr) and 9 (827.93 ± 137.81 ng/mg Cr) postpartum. T 390
 levels were higher at week 9 postpartum than at any other 391
 peripartum time point. Peripartum urinary T excretion varied 392
 significantly among weeks [$F(12, 60) = 7.19, P < 0.01$]. 393
 Significant ($P < 0.05$) between-weeks differences in urinary 394
 T levels are illustrated in Fig. 2 (top panel). 395

Urinary T excretion was related to the timing of females' 396
 postpartum conception. When females conceived DPID, 397
 their overall urinary T concentrations were significantly 398
 higher (523.68 ± 38.74 ng/mg Cr) than at breeding attempts 399
 in which the same females conceived APID [$388.33 \pm$ 400
 27.56 ng/mg Cr; $F(1, 5) = 7.37, P = 0.04$]. Although the 401
 main effects of peripartum week and conception condition 402

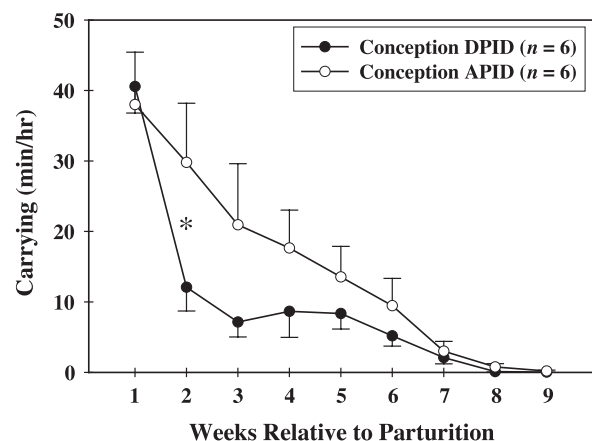


Fig. 1. Mean (\pm SEM) maternal carrying effort when females conceived DPID and APID, $*P < 0.05$.

t2.1 Table 2
t2.2 Mean (\pm SEM) maternal carrying effort and urinary T excretion by timing of conception

Female ID	Carrying effort ^a (min/h)		Peripartum urinary T ^b (ng/mg Cr)	
	Conception DPID	Conception APID	Conception DPID	Conception APID
Bas	8.90 \pm 5.48	<12.52 \pm 4.62	267.62 \pm 36.68	>265.19 \pm 45.51
Bon	7.51 \pm 4.29	>7.31 \pm 2.15	524.39 \pm 60.80	>467.25 \pm 75.72
Jin	13.27 \pm 4.80	<14.35 \pm 4.15	696.70 \pm 115.56	>344.20 \pm 29.93
Luc	6.74 \pm 2.79	<7.62 \pm 4.76	367.60 \pm 31.97	>243.34 \pm 57.85
Pix	12.25 \pm 5.15	<29.94 \pm 8.27	845.82 \pm 130.48	>666.41 \pm 63.57
Xux	7.51 \pm 3.68	<17.18 \pm 6.97	439.98 \pm 45.92	>343.61 \pm 53.33
Mean \pm SE	9.36 \pm 1.77	14.82 \pm 2.39	523.69 \pm 38.74	388.33 \pm 27.56
Concept ^c	NS		0.042	
Wks ^d	0.001		0.001	
Concept \times Wks ^e	0.03		NS	

t2.16 ^a Mean (\pm SEM) carrying effort during postpartum weeks 1–9.
t2.17 ^b Mean (\pm SEM) urinary T excretion during the peripartum period, week –4 prepartum through week 9 postpartum.
t2.18 ^c Concept, main effect for conception condition; numerical value indicates significance (*P*) level; NS, not significant.
t2.19 ^d Wks, main effect for post- and peri-partum weeks.
t2.20 ^e Concept \times Wks, interaction between conception condition and weeks relative to parturition.

403 were significant and the interaction was not, different levels
404 of T excretion for females in each condition can be
405 accounted for by postpartum changes in T excretion that
406 occurred after week 1 postpartum (Fig. 2, bottom panel).
407 Individual data for each female are presented in Table 2. All

426 six females had higher urinary T levels when they conceived
427 DPID than when they conceived APID.
428 *Urinary testosterone excretion and maternal caregiving*
429 *behavior*

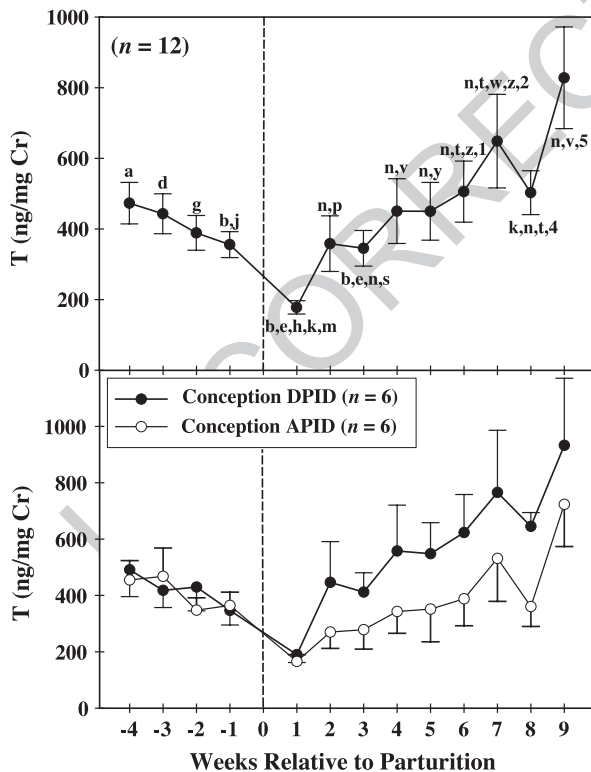


Fig. 2. Data are presented relative to the week of parturition (week 0), which is indicated by the dashed vertical line. [top panel] Mean (\pm SEM) peripartum concentrations of excreted urinary T for all females. Weeks demarked by consecutive letters (e.g., a–b, d–e) or numbers (e.g., 1–2, 4–5) differ significantly from one another, *P* < 0.05. [bottom panel] Mean (\pm SEM) peripartum concentrations of excreted urinary T when females conceived DPID and APID, **P* < 0.05.

430 Urinary T excretion during the postpartum period was
431 related to concurrent maternal behavior. Females' weekly
432 postpartum urinary T concentrations were negatively and
433 significantly correlated with their carrying effort of females
434 during the same postpartum week [*r*(108) = –0.29, *P* =
435 0.002]. Individual Pearson correlation coefficients, by
436 female, are presented in Table 3, along with associated *P*
437 values. In all six females, maternal caregiving effort
438 decreased as urinary T levels increased. For three females
439 (Bon, Pix, and Xux), the relationship between urinary T
440 levels and carrying effort was highly significant (*P* \leq 0.01).
441 For two females, this relationship approached statistical
442 significance (*P* \leq 0.07).

443 **Discussion**

444 A growing body of literature (e.g., Cawthorn et al.,
445 1998; Chandler et al., 1994; Clark et al., 1992a,b, 1997;

t3.1 Table 3
t3.2 Correlations between weekly postpartum urinary T excretion and concurrent maternal carrying effort for each female

Female ID	<i>n</i>	<i>r</i>	<i>P</i>
Bas	18	–0.44	0.07
Bon	18	–0.57	0.01
Jin	18	–0.45	0.06
Luc	18	–0.24	0.34
Pix	18	–0.70	0.001
Xux	18	–0.67	0.003
Mean <i>r</i>		–0.51	t3.10

446 Hegner and Wingfield, 1987, Raouf et al., 1997; Stoehr
447 and Hill, 2000) has provided empirical support for
448 Ketterson and Nolan's (1994, 1999) proposal that male
449 birds and mammals maximize their reproductive success
450 by making T-mediated trade-offs between investment in
451 current and future offspring. The results of our study
452 suggest that females might do the same. When female
453 marmosets conceived APID, during which time their
454 infants were not being nursed or carried as intensively,
455 maternal carrying effort gradually declined across the
456 postpartum period. Yet, when the same females conceived
457 DPID and gestation was coupled with lactation, they
458 abruptly and significantly reduced the amount of time
459 spent carrying their current litters, leaving the care of their
460 2-week-old litters to other family-group members.
461 Although our data are correlational in nature, two analyses
462 provide converging evidence consistent with the hypoth-
463 esis that T regulates maternal behavior. First, the decrease
464 in maternal responsiveness was accompanied by signifi-
465 cantly higher levels of urinary T excretion, relative to
466 breeding attempts in which females conceived APID.
467 Second, mean weekly urinary T levels were found to be
468 negatively and significantly correlated with concurrent
469 carrying effort. Therefore, it appears that the litter-to-litter
470 variation in maternal caregiving effort we observed was
471 reflective of a T-mediated shift of investment away from
472 females' current litters and toward their developing fetuses,
473 in the face of elevated costs associated with producing and
474 caring for offspring.

475 Although the results of our study seem to suggest that the
476 timing of females' postpartum conception affected maternal
477 caregiving behavior, perhaps via modulation of T excretion,
478 Ziegler et al. (1990) reported that in cotton-top tamarins
479 variation in the timing of the postpartum ovulation was a
480 consequence of variation in nursing effort (but also see
481 French, 1983; Lunn and McNeilly, 1982; McNeilly, 1979;
482 Sousa et al., 1999). In our study, we did not record the
483 amount of time spent nursing, due to the difficulty of
484 distinguishing between "time on the nipple" and suckling.
485 Therefore, we were unable to address the possibility that
486 variation in maternal care was the cause, rather than the
487 consequence, of variation in the timing of the postpartum
488 conception. We are quite confident that variation in litter
489 size did not affect our results, however, because singleton
490 and twin litters were equally distributed across both
491 conditions.

492 To the best of our knowledge, the possibility that T
493 might mediate trade-offs between current and future
494 offspring in individual female mammals has not been
495 investigated prior to this study. In our study, individual
496 female marmosets had significantly higher urinary T
497 levels when they conceived DPID than when they
498 conceived APID. Moreover, differences in T levels for
499 the females in each condition could be accounted for by
500 changes in T excretion that occurred 2 weeks postpartum
501 and later—the time of postpartum conception for females

in the DPID condition. Urinary T levels were not only 502
significantly and negatively correlated with concurrent 503
maternal carrying effort, but they were also lowest at 504
week 1 postpartum, when mothers provided the most care 505
for their current litters. These results are particularly 506
exciting in light of reports by Nunes et al. (2000, 2001) 507
that variation in the urinary T levels of male marmosets 508
corresponded to changes in their reproductive effort. For 509
instance, male T levels were at high, prepartum levels, 510
during the first 2 weeks postpartum when males mate 511
most frequently with their female partners. And, as one 512
might expect, T levels decreased significantly, and were at 513
their lowest levels, during the period of maximum 514
paternal caregiving effort (weeks 3–4 postpartum). More- 515
over, as the weaning period progressed, urinary T levels 516
returned to prepartum levels. It seems, then, that the 517
transition from predominantly maternal care to predom- 518
inantly paternal care, which occurs approximately 2 weeks 519
postpartum in *C. kuhlii* families (Fite et al., submitted for 520
publication; Nunes et al., 2000), is regulated by changes 521
in the T levels of males and females. Our results are also 522
in line with reports that, in fish (e.g., Knapp et al., 1999), 523
birds (e.g., Richard-Yris et al., 1987; Wingfield and 524
Farner, 1987), and mammals (e.g., Bridges et al., 1982; 525
Fleming et al., 1997; González-Mariscal, 2001; Strott et 526
al., 1974), T levels decrease with the onset of maternal 527
care and/or exposure to offspring. The results of our 528
study, therefore, indicate a high degree of similarity in the 529
relationship between T and parental effort in male and 530
female marmosets, and shed light on one proximate 531
mechanism by which transitions in female reproductive 532
behavior might be regulated. 533

534 The results of our study indicated that conception DPID 534
coincided, to the week, with both behavioral and 535
endocrinological changes in marmoset females. When 536
females conceived DPID (i.e., during the second post- 537
partum week), they exhibited a significant reduction in 538
carrying effort and elevated urinary T levels during week 2 539
postpartum, relative to when they conceived APID. 540
Unfortunately, we were unable to address the precise 541
timing, to the day, of conception, or the precise timing of 542
changes in maternal behavior and T excretion. While it is 543
possible that changes in maternal behavior may have 544
preceded early conception, and that elevated T levels may 545
have preceded early conception, we do know that female 546
primates exhibit increases in serum androgens early in 547
gestation (see review in Castracane et al., 1998), and that 548
there is reason to believe that T inhibits maternal care 549
(e.g., Bridges et al., 1982; Fleming et al., 1997; González- 550
Mariscal, 2001; Ichikawa and Fujii, 1982; Juárez et al., 551
1998; Knapp et al., 1999; Quadagno and Rockwell, 1972; 552
Richard-Yris et al., 1987; Strott et al., 1974; Wingfield and 553
Farner, 1978), as it does paternal care in some males. 554
Further research on the psychobiological precursors and 555
consequences of variation in the timing of conception will 556
shed light on the exact nature of the within-female 557

558 interactions between maternal physiology and behavior,
559 and encourage investigations into potential fitness con-
560 sequences of these processes.

561 Although our study did not specifically address the
562 issue of the origin of elevated urinary T in females
563 postpartum, it is a central question that bears on the
564 interpretation of the results. If elevated T simply represents
565 peripheral metabolism of steroid precursors prior to
566 excretion, then our measure of urinary T has little
567 relevance to the possibility that circulating T acts on
568 neural circuits critical for maternal motivation and care.
569 However, we have demonstrated that experimental mod-
570 ification of circulating concentrations of plasma T in
571 female marmosets produces the expected changes in levels
572 of excreted T (Armstrong et al., 2003). Further, there is
573 compelling comparative evidence that the differences we
574 noted in androgen production in female marmosets on the
575 basis on postpartum conception status represents a
576 common process in a number of mammalian species.
577 Androgen production [both androstenedione (A_4) and T] is
578 higher in the luteal phase of conceptive ovulatory cycles
579 than in the luteal phase if nonconceptive cycles in dogs,
580 baboons, and human females (Castracane and Goldzieher,
581 1983; Castracane et al., 1998; Concannon and Castracane,
582 1985). In the case of human females, dehydroepiandro-
583 sterone sulfate (an androgen of primarily adrenal origin;
584 Burger, 2002) levels did not differ between conceptive and
585 nonconceptive studies, suggesting that the differences in
586 luteal T and A_4 as a function of conception status reflects
587 differences in ovarian and/or luteal androgen production
588 (Castracane et al., 1998).

589 Even though male and female parental behaviors are
590 thought to be mediated by common neuroendocrinological
591 underpinnings (e.g., Kelley, 1988; Rosenblatt and Ceus,
592 1998; Wynne-Edwards, 2001; Wynne-Edwards and
593 Reburn, 2000), investigations into the role of T in the
594 expression of female reproductive behavior have largely
595 focused on T's influence on sexual behavior. Thus, the
596 possibility that T might also play an important role in the
597 expression of maternal behavior, as it affects the expression
598 of paternal behavior (e.g., Ketterson and Nolan, 1994,
599 1999), has remained largely unexplored. In the study
600 presented here, we examined changes in maternal care-
601 giving behavior, and concurrent T excretion, in female
602 marmosets faced with the costs of gestation coupled with
603 lactation. Not surprisingly, the results of this study suggest
604 that patterns of maternal caregiving behavior were sensitive
605 to the costs of producing and caring for offspring.
606 Furthermore, our results suggest that females, like males,
607 may make trade-offs between investment in current and
608 future offspring, and that elevated urinary T excretion
609 accompanies shifts of marmoset maternal investment away
610 from current offspring and toward developing fetuses. It
611 may be, then, that the expression and regulation of male
612 and female parental behavior is even more analogous than
613 previously recognized.

Uncited references

Altmann and Samuels, 1992	615
Bales et al., 2001	616
Bales et al., 2002	617
Fairbanks and McGuire, 1995	618
González-Mariscal and Rosenblatt, 1996	619
Hauser and Fairbanks, 1988	620
Hrdy, 1994	621
Lee, 1984	622
Lee and Gotlib, 1991	623
Loudon et al., 1984	624
Smith, 1987	625
Tardif and Jaquish, 1997	626

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627
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