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## 2 Effects of social status, age, and season on androgen and cortisol levels in 3 wild male golden lion tamarins (*Leontopithecus rosalia*)

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11

### 12 Abstract

13 This study examines factors affecting androgen and cortisol levels in wild, male golden lion tamarins (*Leontopithecus rosalia*). Golden  
14 lion tamarins are a cooperatively breeding species in which groups often contain two potentially breeding males. Brothers frequently emigrate  
15 together and develop a clear dominance hierarchy, but interactions between them are primarily affiliative. Duos in which the males are not  
16 related are less stable. In addition, reproductive skew theory predicts that dominant males will be less likely to share reproduction with related  
17 subordinates. As such, we predicted that both androgens and cortisol would be higher in subordinate males unrelated to the dominant male.  
18 We also predicted that androgens in breeding males would be higher during the mating season than the birth/infant care season, as per  
19 Wingfield's "challenge hypothesis" (1990). Fecal samples were collected from 24 males in 14 social groups and assayed by enzyme  
20 immunoassay. Androgen levels were higher in breeding males during the mating season, thus supporting the challenge hypothesis. However,  
21 while subordinate males unrelated to the dominant male had significantly lower androgens than any other group, cortisol levels were not  
22 correspondingly higher. These results suggest that unrelated subordinate males show measurable reproductive suppression and may use  
23 strategies such as infantilization to avert aggression from dominant males.

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26 **Keywords:** Androgens; Cortisol; Cooperative breeding; Challenge hypothesis; Tamarin; Reproductive skew

27

### 28 Introduction

29 The regulation of hormones and fertility by various cues  
30 such as social status, age, and season has been studied in  
31 several mammalian and avian species. Steroid hormones,  
32 principally androgens and glucocorticoids, are of particular  
33 interest when studying males because of the dependence of  
34 sexual behavior and spermatogenesis on testosterone and  
35 other androgens (Bronson, 1989; Nelson, 1995) and the  
36 potential of the "stress" hormone cortisol to alter gonadal

function, and hence, reproductive potential (Bronson, 1989; 37  
Sapolsky, 1985). 38

Much research on context-specific differences in steroid 39  
hormones has focused on predictions derived from two 40  
related theoretical positions. The "challenge hypothesis" 41  
(Wingfield et al., 1990) predicts that seasonal changes in 42  
testosterone will vary based on social system, level of 43  
male–male aggression, competition for reproduction, and 44  
presence of estrus females. The "trade-off hypothesis" 45  
(Ketterson and Nolan, 1999), in turn, proposes that 46  
testosterone concentrations in males of biparental species 47  
reflect a trade-off between the male reproductive effort 48  
directed toward mating vs. parental effort. Together, these 49  
hypotheses predict that monogamous, biparental males will 50  
show increased testosterone when male–male conflict is 51

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52 higher and females in estrus are present and decreased  
53 testosterone during times when it is unnecessary or  
54 incompatible with other behaviors, such as infant care.  
55 Although these predictions have been tested widely in avian  
56 systems, several mammalian species have also been used to  
57 evaluate these hypotheses, including spotted hyenas (*Cro-*  
58 *cuta crocuta*: [Goymann et al., 2003](#)); ring-tailed lemurs,  
59 *Lemur catta* ([Cavigelli and Pereira, 2000](#)); and rhesus  
60 macaques (*Macaca mulatta*: [Rilling et al., 2004](#)). Male  
61 tufted capuchins (*Cebus apella nigritus*), in contrast to the  
62 above species which showed support for this hypothesis,  
63 had peaks in testosterone during times of relatively low  
64 aggression ([Lynch et al., 2002](#)). Conforming to predictions,  
65 testosterone dropped during the expression of paternal care  
66 in biparental hamsters (*Phodopus campbelli*), but there was  
67 no similar drop in non-paternal hamsters, *P. sungorus*  
68 ([Reburn and Wynne-Edwards, 1999](#)); testosterone was also  
69 low during the period of high infant care in male Wied's  
70 tufted-ear marmosets, *Callithrix kuhli* ([Nunes et al., 2000](#)).  
71 However, research from other species indicates that elevated  
72 testosterone is compatible with male parental behavior and  
73 may in fact facilitate paternal responsiveness ([Trainor and](#)  
74 [Marler, 2002](#)).

75 One factor confounding interpretation of the association  
76 between androgens and male aggressive behavior is  
77 potential inequity in a social dominance hierarchy. A  
78 relationship between androgens and rank has been found in  
79 some species but not in others. For example, testosterone  
80 was related to dominance rank in immigrant (sexually  
81 active) spotted hyena males in one study ([Holekamp and](#)  
82 [Smale, 1998](#)), but not another ([Goymann et al., 2003](#));  
83 however, the second study included two natal males as well  
84 as the immigrant males. A number of primate studies,  
85 mostly in species characterized by multi-male/multi-female  
86 mating systems, found a positive relationship between  
87 testosterone and dominance rank ([Bercovitch, 1993](#); [Kraus](#)  
88 [et al., 1999](#); [Muller and Wrangham, 2003](#)). But, other  
89 studies have failed to find this relationship ([Lynch et al.,](#)  
90 [2002](#); [Ostner et al., 2002](#); [Sannen et al., 2004](#); [van Schaik](#)  
91 [et al., 1991](#)).

92 In cooperatively breeding mammals, the relationships  
93 between dominant and subordinate breeders, especially  
94 males, are often relatively non-aggressive and primarily  
95 affiliative ([Baker et al., 1993](#); [Garber, 1997](#); [Goldizen,](#)  
96 [1989](#)). In these cases, one might not expect physiological  
97 suppression of reproduction or differences in androgens  
98 between dominants and subordinates. A second view,  
99 however, is predicted by reproductive skew theory  
100 ([Emlen, 1995](#)), which states that dominants should be  
101 less likely to share reproduction with relatives, who get  
102 indirect fitness benefits and are therefore more likely to  
103 stay as helpers. Neither subordinate male high-veld mole-  
104 rats (*Cryptomys hottentotus pretoriae*) nor dwarf mon-  
105 gooses (*Helogale parvula*) demonstrated physiological  
106 suppression of reproduction or rank-related differences in  
107 androgens ([Creel et al., 1992](#); [van Rensburg et al., 2003](#));

108 however, in naked mole-rats (*Heterocephalus glaber*), 108  
109 dominant males had higher testosterone ([Clarke and](#) 109  
110 [Faulkes, 1998](#)). In captive male cotton-top tamarins 110  
111 (*Saguinus oedipus*) and common marmosets (*Callithrix* 111  
112 *jacchus*), natal males housed in the presence of an older, 112  
113 breeding male showed no physiological signs of repro- 113  
114 ductive suppression ([Baker et al., 1999](#); [Ginther et al.,](#) 114  
115 [2002](#)). 115

116 Social relationships may also factor into the regulation 116  
117 of the “stress” hormone cortisol. In a meta-analysis of 117  
118 primate studies, [Abbott et al. \(2003\)](#) examined the relation- 118  
119 ship between dominance status and activity in the 119  
120 hypothalamic–pituitary–adrenal (HPA) axis. Factors iden- 120  
121 tified with higher levels of cortisol for subordinates 121  
122 included higher rates of stressors and lower rates of social 122  
123 support. In contrast, in those species and situations where 123  
124 subordinates experienced lower exposure to potential 124  
125 stressors and/or had higher levels of social support, 125  
126 subordinates tended to have cortisol levels similar to those 126  
127 of dominant individuals. In general, cooperative breeders 127  
128 demonstrate high levels of social support and low levels of 128  
129 stressors. However, the relationship between rank and 129  
130 cortisol might be expected to differ depending on the 130  
131 relatedness of the subordinate, if this also affects social 131  
132 support and stress levels. If stressors and high levels of 132  
133 glucocorticoids are the mechanism for suppression of 133  
134 reproduction, the relationship between cortisol and social 134  
135 rank might be expected to differ across species, depending 135  
136 on whether subordinate males are reproductively sup- 136  
137 pressed ([Bronson, 1989](#)). There was no difference in 137  
138 cortisol between dominant and subordinate males in Wied's 138  
139 marmosets ([Schaffner and French, 2004](#)), naked mole-rats 139  
140 ([Clarke and Faulkes, 1998](#)), rhesus macaques ([Bercovitch](#) 140  
141 [and Clarke, 1995](#)), cotton-top tamarins ([Ginther et al.,](#) 141  
142 [2002](#)), or tufted capuchins ([Lynch et al., 2002](#)), although 142  
143 male capuchins did display increases in cortisol during the 143  
144 time of highest female sexual activity. In a study of wild 144  
145 chimpanzees, dominant males had higher cortisol ([Muller](#) 145  
146 [and Wrangham, 2003](#)). 146

147 Golden lion tamarins (*Leontopithecus rosalia*) are 147  
148 arboreal, New World primates of the family Callitrichidae 148  
149 ([Mittermeier et al., 1988](#)). Golden lion tamarins and other 149  
150 callitrichid primates are characterized by a cooperatively 150  
151 breeding social system which has been variously charac- 151  
152 terized as monogamy ([Kleiman, 1977, 1978b](#); [Baker et al.,](#) 152  
153 [1993, 2002](#)) or cooperative polyandry ([Goldizen, 1987](#); 153  
154 [Sussman and Garber, 1987](#)). Golden lion tamarin groups 154  
155 frequently contain two adult males that are unrelated to the 155  
156 breeding female ([Baker et al., 2002](#)). While both copulate 156  
157 with her, access to the female during estrus periods is 157  
158 monopolized by the behaviorally dominant male ([Baker et](#) 158  
159 [al., 1993](#)). Brothers often emigrate together from their natal 159  
160 groups ([Baker and Dietz, 1996](#)) and enter a new group as 160  
161 the dominant and subordinate breeding pair. In addition, if a 161  
162 breeding female dies and a new female enters a group, a 162  
163 father and son will often both breed with the new female, 163

164 forming a subordinate and dominant duo (Baker et al.,  
165 2002). In one study, 75.7% of observed male breeding duos  
166 were close relatives (Baker et al., 2002), with the remaining  
167 24.3% of duos consisted of unrelated males. Male duos  
168 were stable over time, with observed durations ranging from  
169 1 month to 68 months (Baker et al., 2002).

170 The distinction between male duos that are related vs.  
171 those that are unrelated is biologically important for several  
172 reasons. Golden lion tamarin duos consisting of unrelated  
173 males tended to be less stable (Baker et al., 2002). Most  
174 research on captive male callitrichids has found no differ-  
175 ences in androgens or cortisol levels between related males  
176 of different social statuses. In Wied's tufted-ear marmosets,  
177 levels of urinary testosterone and cortisol did not differ  
178 between dominant and subordinate males in multi-male  
179 groups or with levels found in single males in monogamous  
180 groups (Schaffner and French, 2004). In that study,  
181 polyandrous groups containing unrelated males were  
182 unsuccessful in breeding due to intrasexual aggression  
183 (Schaffner and French, 2004). In male common marmosets,  
184 hormone levels did not differ between fathers and sons  
185 during short tests, whether they were tested with the mother  
186 or an unrelated female present, or whether they were tested  
187 individually or together (Baker et al., 1999). However, in  
188 groups composed of unrelated adult common marmoset  
189 males, subordinate males had lower testosterone (Abbott,  
190 1986, 1993).

191 Golden lion tamarins display markedly seasonal breeding  
192 (Dietz et al., 1994), with most births occurring in October  
193 and November. There is a second, smaller birth peak in  
194 February, which consists mostly of second litters, and no

births in April–July. Second litters are the result of a fertile 195  
post-partum estrus displayed by some females (Bales et al., 196  
2001, Wilson, 1977). Our predictions regarding androgen 197  
and cortisol levels are detailed in Table 1. 198

**Methods** 199

*Subjects* 200

Subjects were 24 male golden lion tamarins in 14 201  
different social groups, free-ranging in Poço das Antas 202  
Biological Reserve (PDA) and outlying reintroduction 203  
areas. James Dietz, Andrew Baker, and colleagues have 204  
monitored approximately 20 groups in the PDA population 205  
since 1983. In all but two cases, the males in the current 206  
study were born in the PDA population and therefore were 207  
of known age and relationship to other animals. All 208  
individuals in the study groups are tattooed and dye-marked 209  
and at least one animal in each group was radio-collared to 210  
facilitate location. 211

Five males were descendants of captive-born animals 212  
reintroduced from zoos (Beck and Martins, 1998). These 213  
males were provisioned three times a week. Descendants of 214  
reintroduced monkeys forage independently and behave in 215  
many respects like native, wild tamarins (Kierulff et al., 216  
2002; Stoinski, 2000). The males included in the present 217  
study did not differ from the PDA males in baseline 218  
androgen ( $n = 24, F_{1,22} = 1.45, P = 0.240$ ) or cortisol levels 219  
( $n = 24, F_{1,22} = 1.05, P = 0.317$ ), and the two groups were 220  
therefore combined for all analyses. 221

t1.1 Table 1

t1.2 Males were placed in six categories according to group composition and predicted levels of intragroup male–male competition

t1.3	Category	Other males besides offspring present	Adult females present	Predicted level of intragroup male competition	Androgen predictions	Cortisol predictions
t1.4	Monogamous	Absent	Unrelated female present	None	High during mating season	Low because social support is high, stressors are low
t1.5	Dominant	Subordinate male present	Unrelated female present	High (although may depend on relatedness of subordinate)	High during mating season	Low because social support is high, although relatedness of subordinate could affect stress levels
t1.6	Subordinate related	Dominant male present (father, brother, or son)	Unrelated female present	High	Low because dominant male should be unwilling to share reproduction	Low because social support is high, stressors are low
t1.7	Subordinate unrelated	Dominant male present (unrelated)	Unrelated female present	High	High because dominant male should be willing to share reproduction	High because social support is low, stressors are higher
t1.8	Natal	Father present	Mother present (no potential mates)	None	Low because there is no potential mate in group	Low because social support is high, stressors are lower

t1.9 Hypotheses and predictions for different categories of males were based on the challenge and trade-off hypotheses, reproductive skew theory, and Abbott et al. (2003).

222 *Collection, extraction, and assay of fecal samples*

223 A total of 196 fecal samples were collected with a mean  
224 of  $8.17 \pm 0.91$  samples per male. Most samples were  
225 collected during four periods: June–July 1996 (preliminary  
226 data), June–November 1997, July–December 1998, and  
227 February–March 1999. Since cortisol concentrations in  
228 feces vary depending on the time of day (Sousa and Ziegler,  
229 1998), we attempted to restrict collection to mornings; 73%  
230 of samples were collected by 12 pm. We used only samples  
231 that were unambiguous as to the identity of the animal of  
232 origin, and we included only one sample per animal per day  
233 in the analyses. Numbers of samples differed between males  
234 due to circumstances such as deaths or the formation of new  
235 study groups. We stored samples at  $-18^{\circ}\text{C}$  until analysis.

236 We allowed fecal samples to thaw at room temperature  
237 and placed 0.125 g fractions of each sample in a round-  
238 bottom 20-ml test tube. We removed seeds, leafy material,  
239 and insect parts from the fecal sample prior to weighing. For  
240 the androgen assay, we solubilized the feces with a 5.0 ml  
241 volume of ethanol and placed the tubes on a shaker rack  
242 overnight (8–12 h). We pelleted the particulate matter in the  
243 resulting slurry by centrifugation for 15 min at 2500 rpm,  
244 poured off the ethanol into clean tubes, and evaporated the  
245 ethanol. We then reconstituted the sample with 1.0 ml  
246 phosphate-buffered saline (PBS) and froze until assay. For  
247 the cortisol assay, we added a 5.0 ml volume of solubilizer  
248 (40% methanol:60% PBS) and placed the tubes on a shaker  
249 rack overnight (12–16 h). We pelleted the particulate matter  
250 in the resulting slurry by centrifugation for 15 min at  
251  $2000 \times g$  and separated the supernatant into a clean test-tube.  
252 We refroze the extracted samples and stored them prior to  
253 assay.

254 *Androgen assay*

255 We measured fecal androgens using an enzyme immuno-  
256 assay previously described (Dloniak et al., 2004; Nunes et  
257 al., 2000) and validated for the golden lion tamarin. The  
258 assay utilized a testosterone antibody (R156/7) and a  
259 testosterone conjugate (horseradish peroxidase; HRP) pro-  
260 vided by William Lasley and Coralie Munro (University of  
261 California, Davis). Assay quality control was monitored by  
262 assaying a lion tamarin fecal extract pool sample on each  
263 plate. The inter-assay coefficient of variation (CV) was  
264 9.0%, and the intra-assay CV was 3.7%.

265 *Cortisol assay*

266 We measured fecal cortisol using an assay previously  
267 characterized (Smith and French, 1997) and validated for  
268 the golden lion tamarin. Intra- and inter-assay coefficients of  
269 variation for a fecal quality control pool were 7.1% and  
270 16.4%, respectively. Cortisol standards and serial dilutions  
271 of extracted feces collected from females at different times  
272 during pregnancy produced parallel displacement curves.

We determined the accuracy of the assay by spiking the  
supernatant of a fecal sample with 100 pg of cortisol  
standard. The recovery of cortisol standard was  $101 \pm 2.0\%$   
( $n = 6$ ).

*Data analyses*

Data were analyzed by mixed-model ANOVA (Littell et  
al., 1996) in Proc Mixed in SAS 8.0 (SAS Institute, Cary,  
NC), with post-hoc analysis by least-squared means.

*Analysis 1*

In the first analysis, fecal androgens and cortisol were  
predicted based on social status, with age of the animal as a  
covariate (Table 2). Data were log-transformed in order to  
meet assumptions of parametric tests. Because 6 animals  
had samples in more than one social status, the animal  
identity was included as a random factor but was eliminated  
when it was not significant. The one male sampled who was  
dominant to an unrelated male was combined in all analyses  
with males dominant to related males.

Behavioral dominance was assessed based on arch-  
walks, mounts, and chases (Baker et al., 1993, 2002).  
Males were grouped into five categories (see Table 1). The  
analysis for each hormone was carried out a second time  
excluding former dominant males who had become sub-  
ordinate on the basis that they might have started out with  
higher steroid levels than other males.

*Analysis 2*

For analysis of androgens and cortisol by season, males  
not in breeding positions (i.e., natal males) were excluded  
from the analysis. Samples from males in breeding positions  
were categorized into mating season (mid-May through late  
July) or birth/infant care season (early September through  
late November) samples. Due to the small sample size  
available during these relatively short periods, dominant/  
monogamous males were combined and subordinate related  
males were combined. Data were then analyzed by mixed-  
model ANOVA with season, social status, and a season by  
social status interaction.

Some females may undergo a post-partum estrus in the 2  
weeks following a birth. This is a period characterized by  
high infant dependency. Only a limited number of samples

Table 2

Independent variables included in models used in each analysis

	Independent variables included in models	
Analysis 1	Status (monogamous, dominant, subordinate/related, subordinate/unrelated, natal)	t2.4
	Age	t2.5
Analysis 2	Status (monogamous/dominant vs. subordinate)	t2.6
	Season (mating vs. birth)	t2.7
	Season by status interaction	t2.8



313 ( $n = 4$ ) were available from males during this period. The  
 314 means of these samples did not differ significantly from the  
 315 other samples collected during the birth/infant care season  
 316 (testosterone:  $F_{1,16} = 3.29$ ,  $R^2 = 0.17$ ,  $P = 0.089$ ; cortisol:  
 317  $F_{1,16} = 0.15$ ,  $R^2 = 0.01$ ,  $P = 0.704$ ). They were therefore  
 318 included with the other samples in the analysis of season. It  
 319 is notable that androgen levels, which exhibited a non-  
 320 significant trend in the above analysis, were lower in the  
 321 post-partum estrus samples ( $45.86 \pm 18.05$  ng/ml) than in  
 322 the birth season samples as a whole ( $113.54 \pm 41.05$  ng/ml).

### 323 Paired tests

324 In some cases, data were available on the same males in  
 325 different categories. Because the sample sizes in these cases  
 326 were small (5–7 males), paired tests were carried out using  
 327 non-parametric Wilcoxon signed-rank tests (Sokal and  
 328 Rohlf, 1981).

## 329 Results

### 330 Androgens

#### 331 Analysis 1: social status, relatedness, and age

332 Fecal androgen values were significantly different  
 333 between categories of different social status ( $F_{5,25} = 3.92$ ,  
 334  $R^2 = 0.44$ ,  $P = 0.0092$ ; Fig. 1). Age was non-significant and  
 335 therefore dropped from the final model. In post-hoc testing,  
 336 we found that males subordinate to an unrelated male had  
 337 significantly lower androgen levels than males in all other  
 338 categories, while natal males also had marginally lower  
 339 androgens than males subordinate to a related male ( $t =$   
 340  $-1.83$ ,  $P = 0.079$ ). Removal of former breeding males who  
 341 then became subordinates (and therefore might be expected to  
 342 start out with higher androgens than a subordinate male  
 343 which had never been in a breeding position) also did not  
 344 change the results, with a new mean for subordinate-related  
 345 males of  $156.34 \pm 70.1$  ng/g feces.

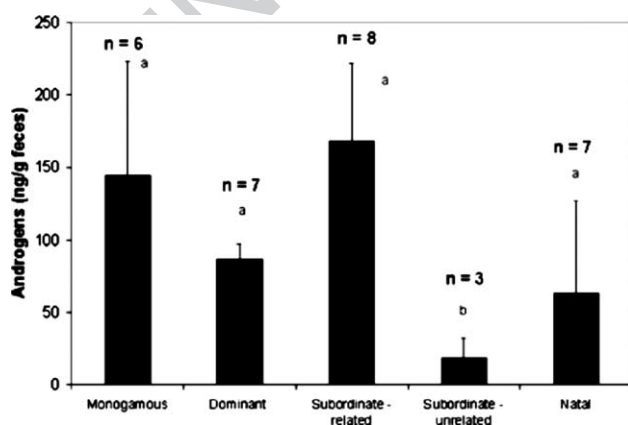


Fig. 1. Mean androgens ( $\pm$ standard error) by male status ( $F_{5,25} = 3.92$ ,  $R^2 = 0.44$ ,  $P = 0.0092$ ). Bars with the same letters are not significantly different.  $n$  = number of males in each category.

#### Analysis 2: social status, season, and status/season interactions

Both social status (monogamous/dominant vs. subordinate) and the status/season interaction were non-significant and therefore dropped from the final model. Androgens did vary significantly by reproductive season, with higher levels of fecal androgens during the mating season than during the birth/infant care season ( $F_{1,24} = 6.80$ ,  $R^2 = 0.22$ ,  $P = 0.015$ ; Fig. 2).

Seven males had samples available from both seasons, and these were also compared within individual males using a paired test. Six out of seven individual males for which both mating and birth season values were available had higher fecal androgens during the mating season (Wilcoxon signed-rank,  $S = 13.0$ ,  $P = 0.031$ ).

### Cortisol

#### Analysis 1: social status, relatedness, and age

Mean levels of fecal cortisol differed among the categories of males (Fig. 3), with the highest levels exhibited by natal males. However, the overall ANOVA for cortisol values showed no significant difference among categories, as well as no difference due to age (overall model:  $F_{6,22} = 1.33$ ,  $R^2 = 0.27$ ,  $P = 0.285$ ). Removal of former breeding males that were now subordinates did not change the results, with a new mean for subordinate-related males of  $374.5 \pm 181.4$  ng/g feces. A paired test on the five males who moved from their natal groups to breeding positions revealed higher concentrations in the natal category than in the breeding category (natal:  $758.06 \pm 178.91$  ng/g; breeding:  $114.78 \pm 27.12$  ng/g), a difference that was marginally significant (Wilcoxon signed-rank,  $S = 7.5$ ,  $P = 0.062$ ).

#### Analysis 2: social status, reproductive season, and status/season interactions

Both status (monogamous/dominant vs. subordinate) and the status/season interaction were non-significant and therefore dropped from the final model. There was a non-significant trend in all breeding males combined for cortisol to be higher during the birth/infant care season than during the mating season ( $F_{1,24} = 3.68$ ,  $R^2 = 0.133$ ,  $P = 0.067$ ; Fig. 2). Three out of seven individual males for which both mating and birth/infant care season values were available had higher cortisol during the mating season, and four had higher cortisol during the birth season (Wilcoxon signed-rank,  $S = -4.0$ ,  $P = 0.578$ ).

## Discussion

The results of this study add to the growing literature indicating that gonadal function in cooperatively breeding mammals is exquisitely sensitive to subtle aspects of group demography. Androgens in golden lion tamarin males varied

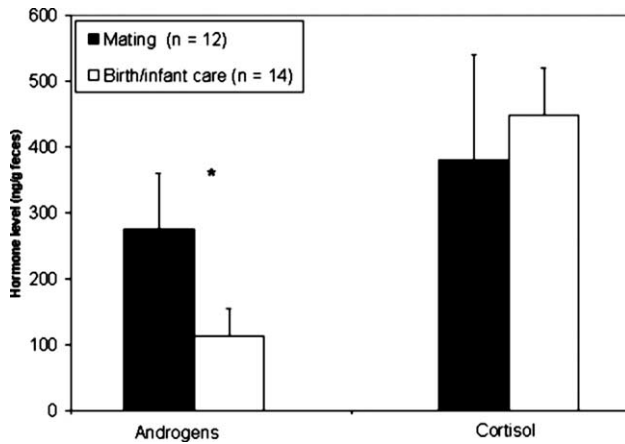


Fig. 2. Mean androgens and cortisol ( $\pm$ standard error) by season ( $*P < 0.05$ ).

396 with social status, reproductive season, and relatedness.  
 397 Only subordinate males unrelated to the dominant male of  
 398 their group showed androgen levels lower than those of  
 399 dominant males; subordinate males that were related to the  
 400 dominant male had levels of fecal androgens that were  
 401 statistically indistinguishable from those of the dominant  
 402 male.

403 Based on studies of captive marmosets and tamarins  
 404 (Möhle et al., 2002; Ziegler et al., 2000), it is likely that  
 405 these androgens were primarily of gonadal rather than  
 406 adrenal origin. It is also notable that, while fecal cortisol  
 407 trends up in the birth/infant care season, androgens are  
 408 significantly lower, suggesting a dissociation between the  
 409 secretory products associated with the hypothalamic–  
 410 pituitary–adrenal axis and the hypothalamic–pituitary–  
 411 gonadal axis. In addition, cortisol did not show significant  
 412 variation according to male status, suggesting that stress- or  
 413 metabolic-induced changes in the hypothalamic–pituitary–  
 414 adrenal axis do not influence the production of androgens in  
 415 subordinate, unrelated males under these conditions. There  
 416 are, however, a number of potential factors (social, environ-  
 417 mental, and physiological) affecting cortisol that we were  
 418 unable to address in this study. Our one finding with regard  
 419 to cortisol is that within individual males there was a trend  
 420 for cortisol to drop when a male moved from his natal group  
 421 to a breeding position. In mammals that form pair-bonds, it  
 422 is common for the formation of a pair-bond to be associated  
 423 with a short- or long-term drop in stress hormones (Carter,  
 424 1998; Ginther et al., 2001; Hoffman, 1998; Mendoza et al.,  
 425 2002; Reburn and Wynne-Edwards, 1999; Schaffner and  
 426 French, 2004). It is interesting that this drop in cortisol when  
 427 entering a breeding position is apparent even when the male  
 428 is entering into a subordinate position and presumably  
 429 engaging in less sexual behavior with the female (Baker et  
 430 al., 1993; Kleiman, 1978a).

431 Androgens also varied according to the predictions of the  
 432 challenge and trade-off hypotheses, being higher during the  
 433 mating season (a period characterized by high levels of  
 434 mate-guarding and male–male interaction, as well as access  
 435 to breeding females). Also as predicted, androgen levels

were lower during the season of high paternal care. These  
 436 data are consistent with those from captive Wied's  
 437 marmosets (Nunes et al., 2000, 2001), in which urinary  
 438 testosterone dropped following post-partum mating, and  
 439 males who carried infants more had lower testosterone.  
 440 Similar results have been found in biparental hamsters  
 441 (Reburn and Wynne-Edwards, 1999) and Mongolian ger-  
 442 bils, *Meriones unguiculatus* (Clark et al., 2004). Nunes et al.  
 443 (2001) also found a negative relationship between cortisol  
 444 and carrying behavior. While we did not find lower cortisol  
 445 in the birth/infant care season, here, we did not consider  
 446 individual variation in hormone levels and infant carrying.  
 447 This would be a valuable analysis to undertake in the future  
 448 when additional samples become available. In addition,  
 449 species have a post-partum estrus during which mating and  
 450 infant care might be expected to produce “competing”  
 451 endocrine responses. Another avenue for future research  
 452 might involve following up on the observation that, in this  
 453 study, male androgen levels tended to be lower during the  
 454 females' post-partum estrus.  
 455

456 The lower androgens in the subordinate of unrelated  
 457 male–male duos might not be unexpected if one predicts  
 458 that high androgens in a subordinate might lead to behavior  
 459 viewed as a challenge by the dominant male. However, this  
 460 finding does run contrary to predictions derived from  
 461 reproductive skew theory (Emlen, 1995). According to this  
 462 body of theory, subordinates to whom the dominant male is  
 463 most closely related receive the largest benefit from helping  
 464 raise the dominant's offspring due to indirect fitness  
 465 benefits. The dominant should therefore be less obliged to  
 466 share reproduction with them in an effort to entice them to  
 467 stay in the group. Our results are clearly in opposition to this  
 468 prediction, showing lower reproductive suppression of  
 469 related males.

470 Several clues suggest that the relationship between  
 471 dominant and unrelated subordinate males is more tenuous  
 472 than that between dominants and related subordinates. Not  
 473 only do unrelated male duos tend to persist for less time in  
 474 this study population of golden lion tamarins (Baker et al.,  
 475

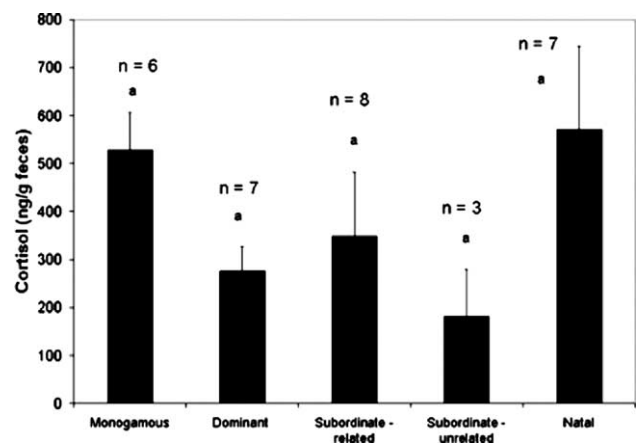


Fig. 3. Mean cortisol ( $\pm$ standard error) by male status. Bars with the same letters are not significantly different.

475 2002), but the formation of unrelated male duos in this and  
 476 other callitrichid species in captivity has been difficult  
 477 (Kleiman, 1978a; Schaffner and French, 2004). Unrelated  
 478 subordinate males may also participate less in certain daily  
 479 activities of the social group, although more field data may  
 480 be necessary to determine this. In a study of captive golden  
 481 lion tamarins, the male that sexually monopolized the  
 482 female also interacted more with her in non-sexual contexts  
 483 (Kleiman, 1978a). Male infant transport may vary according  
 484 to the relatedness of the subordinate; in the one male duo in  
 485 Baker's study in which the subordinate and dominant were  
 486 known to be unrelated, the subordinate carried less than half  
 487 as much as the dominant (Baker et al., 1993). As infant  
 488 transport varied according to relatedness to the infant in  
 489 natal males (Baker, 1991), it is possible that the same is true  
 490 in breeding males. Studies of wild moustached tamarins  
 491 (*Saguinus mystax*) and common marmosets also docu-  
 492 mented large disparities in some groups in the extent to  
 493 which each male carried the infants (Garber, 1997). In  
 494 addition, subordinate males in three out of seven groups  
 495 observed were not seen to copulate at all with the dominant  
 496 female (all dominant males copulated) (Baker et al., 1993),  
 497 although once again it is unclear if relatedness of the  
 498 subordinate was the key difference.  
 499 The overall picture suggests tolerance of unrelated  
 500 subordinate males but less than full integration into the  
 501 group. Animals seeking admission into a group (Bales,  
 502 pers. obs.) and subordinate males following an aggressive  
 503 encounter (Baker et al., 1993) often give infantilized  
 504 calls, probably to avert aggression. Suppression of  
 505 androgens in this context could also be meant to avert  
 506 aggression and could be either a cause or a consequence  
 507 of infantilization.

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523

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