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Social and Reproductive Factors Affecting Cortisol Levels in Wild Female Golden
Lion Tamarins (*Leontopithecus rosalia*)

Karen L. Bales^{1,2,3}, Jeffrey A. French⁴, Caroline M. Hostetler^{1,2,3}, James M. Dietz¹

1. Dept. of Biology, University of Maryland, College Park
2. Dept. of Psychology, University of California, Davis
3. California National Primate Research Center
4. Dept. of Psychology, University of Nebraska, Omaha

Short title: Cortisol in Female Tamarins

Correspondence should be sent to: Karen L. Bales, Dept. of Psychology,
University of California, Davis, CA 95616. Ph: (530) 754-5890; Fax: (530) 752-
2087; email: klbales@ucdavis.edu

1 **Abstract**

2
3 The steroid hormone cortisol has been associated with differing levels of
4 “stress” as well as with differing reproductive conditions in many primates. In
5 captive callitrichids, cortisol has more often been reflective of female reproductive
6 status than of chronic stress. However, endocrine patterns of other steroids have
7 often differed in wild and captive callitrichids. In this study, we addressed the
8 hypothesis that wild golden lion tamarin (*Leontopithecus rosalia*) females would
9 demonstrate patterns of cortisol excretion similar to those seen in captive female
10 callitrichids. We collected and assayed for cortisol 710 fecal samples from 22
11 adult females in Poço das Antas Reserve, Brazil. Differences in cortisol levels
12 were found across the reproductive cycle. Females in their 1st trimester of
13 pregnancy experienced a reduction in cortisol, with a rise in the 3rd trimester.
14 Primiparous females had a higher rise in the 3rd trimester than multiparous
15 females. No differences in cortisol levels were found between dominant females,
16 ovulatory subordinate females, or anovulatory subordinate females. These
17 results are similar to those from captive callitrichid females. The lack of
18 differences in cortisol excretion between dominants and subordinates is likely
19 due to the low levels of overt aggression and high level of social support
20 available to subordinate females. While data are available from captive
21 callitrichid females of other species, cortisol data from captive golden lion
22 tamarins would be helpful in further evaluating this hypothesis.

23 **Key Words** Cortisol, tamarin, callitrichid

24

25

26 In many primate species levels of the steroid hormone cortisol are affected by
27 a number of factors, including social status (Shively et al., 1997; Sapolsky, 1995;
28 Cavigelli et al., 2003; Saltzman et al., 1994), social stability (Sapolsky, 1983;
29 Smith et al., 1997), stressful experiences (Johnson et al., 1996; Albuquerque et
30 al., 2001; Smith and French, 1997a; Smith and French, 1997b), and
31 reproductive state (Ziegler et al., 1995; Ziegler and Sousa, 2002; Weingrill et al.,
32 2004). Cortisol levels can also vary both across and within taxonomic groups
33 (Abbott et al., 2003).

34 Abbott et al. (2003) in a meta-analysis of studies examining the relationship
35 between dominance status and activity in the hypothalamic-pituitary-adrenal
36 (HPA) axis, examined a number of the factors which might predict the ratio of
37 basal cortisol concentrations expressed by subordinates, relative to
38 concentrations expressed by dominants. Factors identified with higher levels of
39 cortisol for subordinates included higher rates of stressors and lower rates of
40 social support. In contrast, in those species and situations where subordinates
41 experienced lower exposure to potential stressors, and/or had higher levels of
42 social support, subordinates tended to have cortisol levels similar to those of
43 dominant individuals. With knowledge of these social parameters, it is possible
44 to make *a priori* predictions regarding relative levels of cortisol for dominants and
45 subordinates in a given primate species. These predictions are confirmed by
46 available data on females from several callitrichid species, most in captivity. In
47 general, rises in cortisol appear to be connected to reproductive events and

48 status rather than to chronic stress: wild female common marmosets, *Callithrix*
49 *jacchus* (Albuquerque et al., 2001); captive cotton-top tamarins (Ziegler et al.,
50 1995); captive common marmosets (Ziegler and Sousa, 2002), and captive
51 Wied's tufted ear marmosets (*Callithrix kuhlii*) (Smith and French, 1997b).
52 However, cortisol in both common marmosets and Wied's tufted-ear marmosets
53 has also been shown to be sensitive to psychogenic stressors caused by
54 experimental manipulations such as changes in the social group (Smith et al.,
55 1997; Johnson et al., 1996), isolation (Smith and French, 1997a; Johnson et al.,
56 1996; Smith and French, 1997b), and manual restraint (Smith and French,
57 1997b) .

58 In this study, we examined cortisol profiles for free-ranging female golden lion
59 tamarins in Rio de Janeiro State, Brazil. Golden lion tamarins (*Leontopithecus*
60 *rosalia*) live in a cooperatively breeding social structure in which (usually) one
61 female breeds with one or more males (Baker et al., 1993). Polygyny occurs in
62 about 10% of group-years and usually involves a mother-daughter pair in which
63 the breeding male has been replaced (Dietz and Baker, 1993). Both males and
64 older offspring help to rear infants. Aggression is rare (rather than continuous)
65 and usually associated with dispersal events, and relationships between
66 subordinate and dominant females are often characterized by high levels of
67 mutual affiliative behavior (Baker et al., 2002). Given the predictors of status
68 differences in cortisol identified by Abbott et al. (2003), then, we would predict
69 that subordinate female lion tamarins would express cortisol levels similar to, or
70 less than, the cortisol concentrations expressed by dominant females.

71 Patterns of female fertility and gonadal steroid excretion vary significantly
72 between wild and captive callitrichid populations. While female golden lion
73 tamarins are not physiologically suppressed from reproduction while in captivity
74 (French, 1987), in wild groups there is evidence of anovulation in some adult,
75 subordinate females (French et al., 2003). It is therefore possible that patterns
76 of cortisol excretion also differ in the wild. There is no published study of cortisol
77 in captive golden lion tamarins, therefore we have had to compare our results to
78 the general patterns found in other callitrichid species. We hypothesized that
79 reproductive status would affect cortisol, while non-reproductive females would
80 demonstrate basal cortisol levels less than or equal to those of dominant females
81 depending on their own reproductive status.

82

83 **METHODS**

84 **Subjects**

85 Subjects were 22 female golden lion tamarins, 17 dominants and 9
86 subordinates (four were represented in both states). Females were free-ranging
87 in Poço das Antas Biological Reserve (PDA) and outlying Reintroduction areas,
88 (Table 1). Drs. James Dietz, Andrew Baker, and colleagues have monitored
89 approximately 20 groups in the PDA population since 1983. All individuals in the
90 study groups are tattooed and dye-marked and at least one animal in each group
91 is radio-collared to facilitate location.

92 Females were classified as dominant if they were the only breeding female in
93 the group, or if they were behaviorally dominant to the other female (based on

94 access to the breeding male, arch-walks, mounts, and chases). Females were
95 classified as ovulatory or anovulatory based on levels of fecal estrogen
96 conjugates and pregnanediol glucoronide (French et al., 2003). Subordinate
97 females, particularly those that were anovulatory, tended to be younger than
98 dominant females: dominant females, age (mean \pm standard error) = 1909.65 \pm
99 289 days; ovulatory subordinates, age = 1443 \pm 386 days; anovulatory
100 subordinates, age = 604 \pm 205 days. However, age was not significantly
101 associated with cortisol levels in an analysis of covariance ($F_{1,24} = 2.33$, $p =$
102 0.14). In addition, the overall pattern of results did not change when samples
103 taken before females were 18 months old were excluded.

104 Four dominant females were descendants of captive-born animals
105 reintroduced from zoos (Beck and Martins, 1998). These females were all born in
106 the wild and were provisioned three times a week. Descendants of reintroduced
107 monkeys are capable of independent foraging and behave in many respects like
108 native, wild tamarins. These females did not differ from the PDA females in
109 baseline cortisol levels ($\chi^2 = 1.191$, $p = 0.2751$), and the two groups were
110 therefore combined for all analyses.

111

112 **Collection, Extraction, and Assay of Fecal Samples**

113 We collected fecal samples approximately twice a week for each female
114 during four periods: June-July 1996 (preliminary data), June-November 1997,
115 July-December 1998, and February-March 1999. Samples were also collected
116 opportunistically during other periods. Since cortisol concentrations in feces vary

117 depending on the time of day (Sousa and Ziegler, 1998), we attempted to restrict
118 sample collection to mornings. Fifty percent of samples were collected by 9:00
119 am and 80% by 12 pm. We used only samples that were unambiguous as to the
120 identity of the animal of origin, and we included only one sample per animal per
121 day in the analysis. Numbers of samples differ between females due to
122 circumstances such as deaths, formation of new study groups, and an
123 unexpected birth by one subordinate female. We stored samples at ~ 18° C until
124 analysis.

125 We allowed fecal samples to thaw at room temperature, and placed 0.125 g
126 fractions of each sample in a round-bottom, 20-ml test tube. We removed seeds,
127 leafy material, and insect parts from the fecal sample prior to weighing. We
128 added a 5.0 ml volume of solubilizer (40% methanol: 60% phosphate buffered
129 saline (PBS)) and placed the tubes on a shaker rack overnight (12-16 hrs). We
130 pelleted the particulate matter in the resulting slurry by centrifugation for 15 min
131 at 2000 g, and separated the supernatant into a clean test-tube. We refroze the
132 extracted samples and stored them prior to assay.

133

134 **Cortisol Assay**

135 We measured fecal cortisol using an assay previously characterized (Smith
136 and French, 1997a). We coated microtiter plates (Nunc Maxisorp F96) with rabbit
137 anticortisol (R4866) diluted 1:12,000 in sodium bicarbonate coating buffer. We
138 further diluted extracted fecal samples with assay buffer (1:10) prior to
139 measurement to place the sample concentration within the range of the standard

140 curve. We diluted cortisol standards (ICN Biomedical, Costa Mesa, California,
141 USA) in a 1:10 dilution of extraction buffer. Cortisol standards ranged from 1000
142 to 7.8 pg/well in halving concentrations. We diluted cortisol-horseradish
143 peroxidase (HRP) conjugate (batch 11/94) in PBS and added it to the wells. After
144 a 2-hr incubation, we washed the plate wells and added hydrogen peroxide and
145 ABTS (2,2'-Azino-bis(3-thylbenzthylene-6-sulfonic acid)) as a chromogen. We
146 measured absorbance at 1 hr later at 410 nm (reference 570 nm) in a Dynatech
147 MR5000 microplate reader, and calculated the sample concentrations using a
148 four-parameter sigmoidal curve fitting function. Intra- and interassay coefficients
149 of variation for high and low concentrations of a fecal quality control pool were
150 6.7 % and 13.6% (high) and 6.1% and 16.0% (low). Cortisol standards and serial
151 dilutions of extracted feces collected from females at different times during
152 pregnancy produced parallel displacement curves. We determined the accuracy
153 of the assay by spiking the supernatant of a fecal sample with 100 pg of cortisol
154 standard. The recovery of cortisol standard was $101 \pm 2.0\%$ (n=6).

155

156 **Data Analysis**

157 Reproductive stage was classified as non-pregnant, 1st, 2nd, or 3rd trimester
158 based on counting backwards (132 days) from parturition and by examination of
159 gonadal steroid levels. Females that produced offspring during the study were
160 also classified as primiparous (first parturition) or multiparous (second or later
161 parturition). Because some of the data were neither normal nor transformable to
162 normality, non-parametric Kruskal-Wallis tests (Sokal and Rohlf, 1981) were

163 used throughout. Due to the use of non-parametric statistics, all data are
164 presented as medians and interquartile ranges.

165

166 **RESULTS**

167 **Effects of Reproductive Status**

168 When compared to non-pregnant levels, cortisol levels dropped significantly
169 during the 1st trimester of pregnancy (Figure 1; Kruskal-Wallis test, $\chi^2 = 7.59$, $p =$
170 0.006). Levels rose slightly but non-significantly in the 2nd trimester compared to
171 the 1st trimester (Kruskal-Wallis test, $\chi^2 = 2.77$, $p < 0.0958$), and then rose
172 significantly during the 3rd trimester of pregnancy (Kruskal-Wallis test, $\chi^2 = 12.31$,
173 $p < 0.0005$), when compared to the 2nd trimester. Primiparous females did not
174 differ from multiparous females during the non-pregnant stage or the first two
175 trimesters, but had significantly higher cortisol levels during the third trimester of
176 pregnancy (Figure 2; Multiparous females = 10; primiparous females = 6;
177 Kruskal-Wallis test, $\chi^2 = 5.69$, $p < 0.017$).

178

179 **Effects of Dominance Status**

180 Four females had non-pregnant cortisol values both as dominants and as
181 subordinates. When these were compared in a paired-sample test, there was no
182 significant difference in cortisol concentrations between statuses (Wilcoxon
183 signed-rank test, NS; Figure 3). When non-pregnant cortisol values were
184 compared for dominant females, ovulatory subordinates, and anovulatory

185 subordinates, no significant differences were found (Kruskal-Wallis test, $\chi^2 =$
186 0.52, $p = 0.7694$; Figure 4).

187

188 **Discussion**

189 Cortisol levels in wild golden lion tamarin females appear to be primarily
190 influenced by reproductive state, as opposed to social status. There is significant
191 variation in cortisol across pregnancy, with a dip in levels in the 1st trimester of
192 pregnancy and then a significant rise in the 3rd trimester. In contrast, dominant
193 and subordinate females did not differ in cortisol levels, even when ovulatory
194 subordinates were compared separately from anovulatory subordinates.

195 These patterns are generally consistent with data from several other
196 callitrichid species, including common marmosets (Ziegler et al., 1995), cotton-
197 top tamarins (Ziegler et al., 1995), and Wied's black tufted-ear marmosets (Smith
198 and French, 1997b). In addition, they fit the predictions of Abbott et al. (2003)
199 based on the golden lion tamarin social system. Wild subordinate female golden
200 lion tamarins have extensive social support within the group, and are subject to
201 only low levels of harassment (culminating near the time of expulsion from the
202 group), and live in groups consisting of close kin (Baker et al., 1993; Dietz and
203 Baker, 1993). In the statistical models generated by Abbott et al. (2003), all of
204 these features were associated with similar or lower levels of baseline cortisol
205 titers in subordinates, relative to dominants. Our results clearly indicate that fecal
206 cortisol concentrations did not differ, either on the basis of social status

207 (dominant vs. subordinate) or on the basis of ovulatory status (anovulatory vs.
208 ovulatory).

209 The elevated third trimester concentrations of cortisol are consistent with
210 results from other callitrichid primates (Smith & French, 1997; Ziegler et al. 1995)
211 and primates in other taxa, including human females (French et al., 2004); also
212 see review in (McLean and Smith, 1999). The finding that primiparous females
213 have higher cortisol in the 3rd trimester of pregnancy is interesting in the light of
214 previous results that subordinate (usually primiparous) mothers had higher rises
215 in estrogen conjugates during pregnancy (French et al., 2003). To the extent that
216 steroidogenesis in lion tamarins is similar to other primates, this result is
217 consistent with the observation that adrenal steroids appear to be critical
218 precursors or prohormones for placental estrogens (Novy and Walsh, 1983;
219 Waddell et al., 1992). Thus, elevated glucocorticoids would provide more
220 substrate for the biosynthesis of estrogens. In our sample, 5 out of 6 primiparous
221 mothers were the dominant female in their group. Subordinate status therefore
222 cannot explain the difference in cortisol levels between primiparous and
223 multiparous mothers. In addition, females with higher rises in cortisol during
224 pregnancy gave birth to larger infants (Bales et al., 2002). It is possible that the
225 difference in fecal cortisol during the 3rd trimester relates either to differential
226 cortisol metabolism in first-time mothers, differential fetal demand upon maternal
227 glucose levels (Haig, 1993) during first pregnancies, or to differential levels of
228 psychological stress experienced by the pregnant female during first vs.

229 subsequent pregnancies. Higher cortisol in first-time mothers might also be
230 involved in sensitization to olfactory cues associated with infants (Leon, 1992).

231 Patterns of female fertility and reproductive suppression vary significantly
232 between wild and captive callitrichid populations, with some wild subordinate
233 golden lion tamarins showing evidence of anovulation. The absence of
234 differences in cortisol levels, however, suggest that, as in captive marmosets
235 (Saltzman et al., 1994; Saltzman et al., 2000), this reproductive suppression is
236 not caused by elevated cortisol levels. Further study of free-ranging females,
237 especially dispersing individuals seeking breeding opportunities, will be useful in
238 disentangling these effects. In addition, cortisol data from captive golden lion
239 tamarins would be valuable in allowing a direct, within-species comparison
240 between wild and captive females.

241

242

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249 thank R. Lake, A. Martins, and the Ecología field team for field assistance. This
250 research complies with the University of Maryland Animal Care and Use
251 committee and all relevant Brazilian laws.

252

253

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337

338 **Figure Legends.**

339

340 Figure 1. Female cortisol (ng/g feces) by stage of pregnancy (median \pm
341 interquartile range).

342

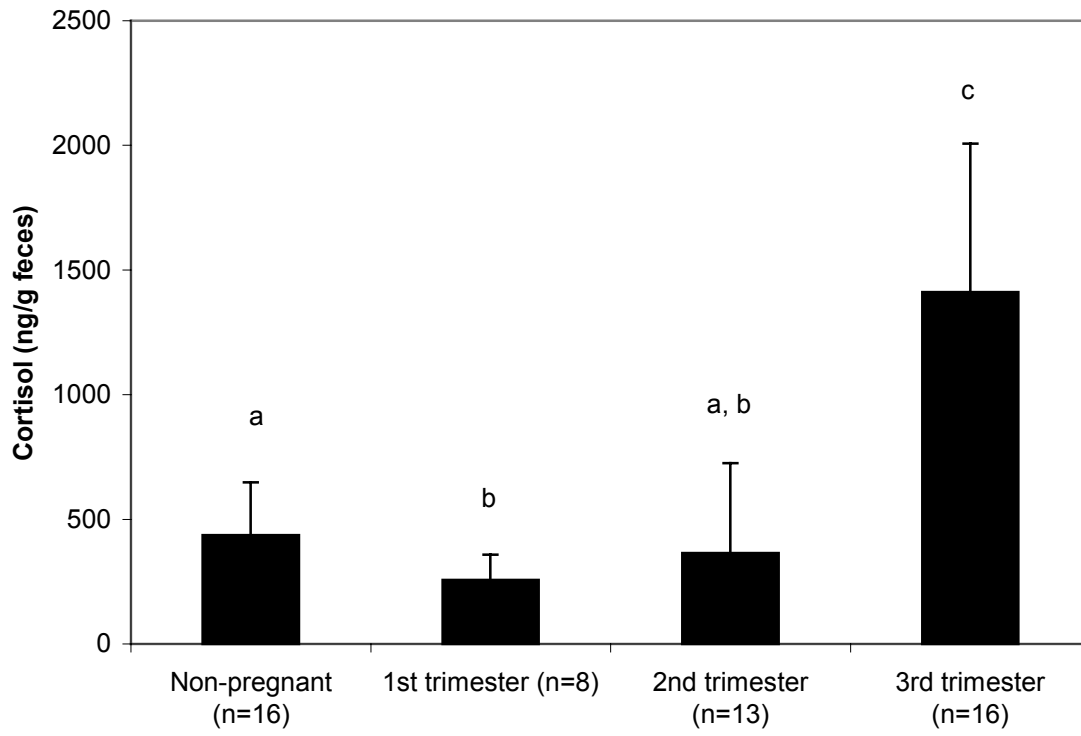
343 Figure 2. Comparison of cortisol (ng/g feces) during different stages of pregnancy
344 in primiparous and multiparous mothers pregnancy (median \pm interquartile
345 range). Numbers above the bars are the sample size for that category. Levels
346 are significantly different only in the third trimester ($\chi^2 = 5.69$, $p < 0.017$).

347

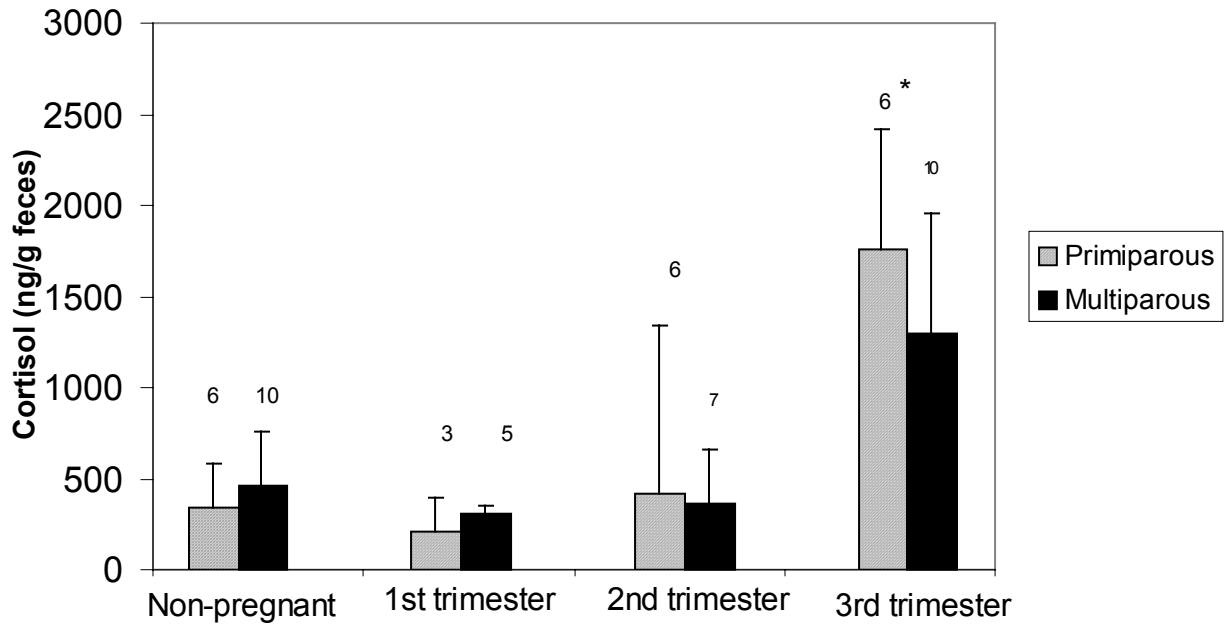
348 Figure 3. Cortisol levels (ng/g feces) for four females that were both dominants
349 and subordinates during the study period (median \pm interquartile range).

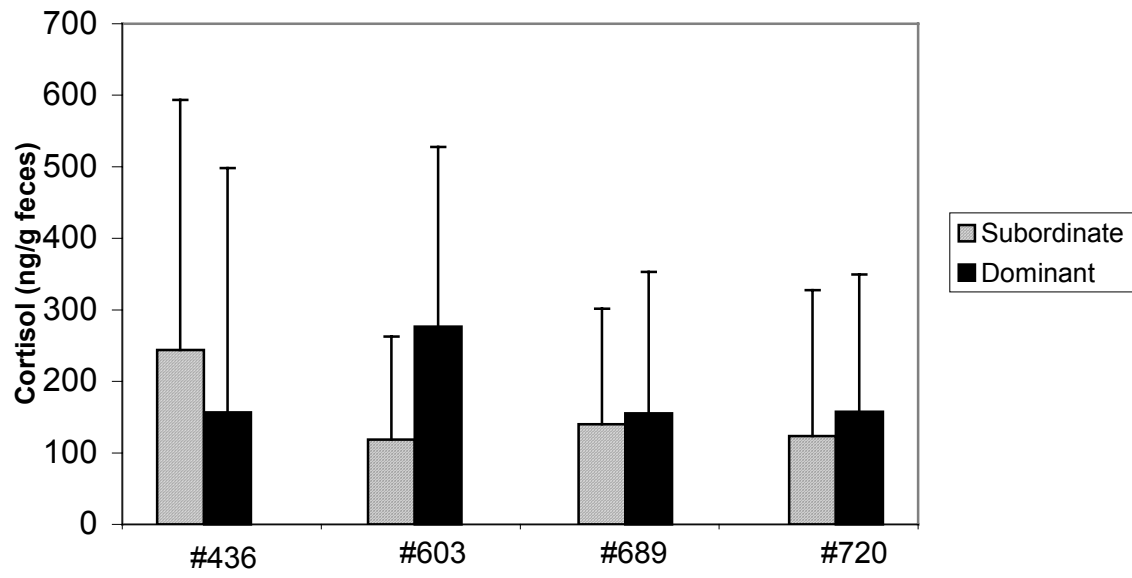
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351 Figure 4. Non-pregnant cortisol levels (ng/g feces) for females according to
352 dominance and reproductive status (median \pm interquartile range).

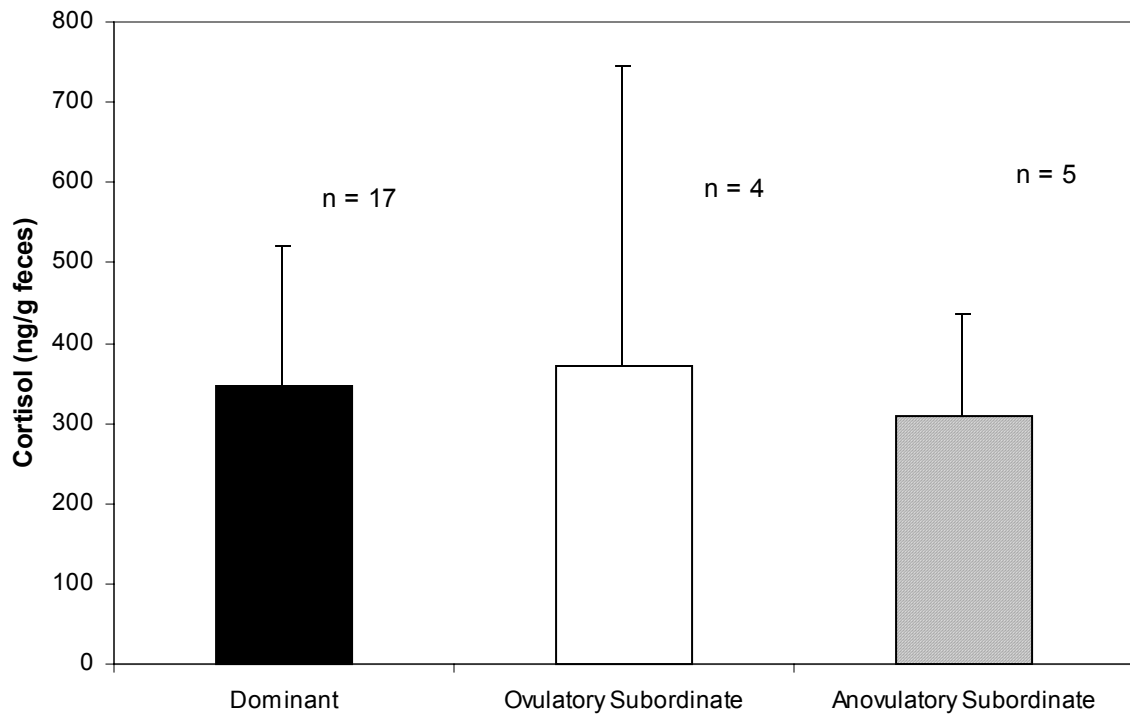


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353



353 Table 1. Details of females and fecal sample sizes used in this study.

354

Female ID	Birthdate	Social Status	Ovulatory Status	Number of Samples
3	Sept 1981	Dominant	Ovulatory	20
291	13 Sept 1988	Dominant	Ovulatory	81
436	25 Nov 1991	Dominant until 10/29/98; then subordinate	Ovulatory in both statuses	79
524	4 Oct 1993	Dominant	Ovulatory	40
539	15 Nov 1993	Dominant	Ovulatory	31
603	30 Sept 1994	Subordinate until 10/29/98; then dominant	Ovulatory in both statuses	67
629	1994	Dominant	Ovulatory	14
650	11 Sept 1995	Subordinate	Ovulatory	23
651	1993	Dominant	Ovulatory	53
672	1993	Dominant	Ovulatory	17
685	14 August 1996	Subordinate	Anovulatory	14
688	5 Nov 1996	Subordinate	Anovulatory	8
689	5 Nov 96	Subordinate until 11/30/98, dominant after 1/19/99	Anovulatory; then ovulatory	37
703	1995	Dominant	Ovulatory	45
704	1994	Subordinate	Ovulatory	5
720	1994	Subordinate until 2/99, then dominant	Anovulatory, then ovulatory	51
721	1994	Dominant	Ovulatory	51
723	15 Nov 1997	Subordinate	Anovulatory	10
CM11	Nov 1992	Dominant	Ovulatory	23
CM13	Nov 1993	Dominant	Ovulatory	12
MA9	Oct 1995	Dominant	Ovulatory	10
ST6	Mar 1993	Dominant	Ovulatory	29
			TOTAL SAMPLES	710

355