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SEXUAL DIFFERENCES IN BEHAVIORAL AND HORMONAL RESPONSES TO SOCIAL CHANGE IN COMMON MARMOSETS *CALLITHRIX JACCHUS*

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Abstract. Changes in the social environment of primates can be very stressful, and the effects may vary according to the sex and age of the animal. The present study investigated the hormonal and behavioral responses to social privation of captive common marmosets (*Callithrix jacchus*) in two experimental groups: (a) 8 adult heterosexual pairs and (a) 9 subadult same-sex twin pairs (M-M = 5; F-F = 4). Focal-animal behavioral sampling was conducted during two phases: baseline (phase 1) and social privation (phase 2 - individual isolation in heterosexual pairs, removal from natal group in twins). Fecal samples were collected simultaneously for analysis of cortisol levels, using ELISA. Significant (ANOVA, *t* test) differences between phases, pairings and sexes were recorded for social behaviors (grooming, piloerection, and scent-marking). Mean cortisol levels increased in phase 2 in both groups and sexes, although levels in the males rose considerably more than in females in both groups. The sum of the behavioral and hormonal evidence indicates that males are affected more adversely by social privation than females. This is interpreted in the context of gender-based differences in the reproductive biology of *C. jacchus*, characterized by competition among females for breeding status, but tolerance among males. Selection pressures may thus have favored greater affiliative attachment among males living in the same social group, which is reflected in higher levels of stress under social privation. Clearly, then, sex, age and social context may all influence an individual's response to changes in the social environment.

Key words: *Callithrix jacchus*, gender differences, stress response, cortisol.

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Resumo. Para os primatas, mudanças no ambiente social podem ser muito estressantes e os efeitos podem variar de acordo com o sexo e a idade dos animais. O presente estudo investigou as respostas comportamentais e hormonais à privação social de sagüi comum cativos (*Callithrix jacchus*) em dois grupos experimentais: (a) 8 pares heterossexuais adultos e (b) 9 pares iso-sexuais de gêmeos sub-adultos (M-M = 5; F-F = 4). Foi utilizado o método focal contínuo para o registro do comportamento durante duas fases: basal (fase 1) e de privação social (fase 2 -isolamento individual para os pares adultos e remoção do grupo familiar para os gêmeos). As amostras de fezes foram coletadas simultaneamente para análise dos níveis de cortisol, utilizando o método ELISA. Foram observadas diferenças significativas (ANOVA, teste *t*) entre as fases, entre tipos de grupo e entre os sexos para os comportamentos sociais (catação, piloereção e marcação-de-cheiro). Os valores médios de cortisol aumentaram na fase 2 em ambos os sexos nos dois tipos de grupo, embora a elevação dos níveis de cortisol nos machos tenha sido maior do que nas fêmeas, em ambos os grupos. Em conjunto, as evidências comportamentais e hormonais indicam que machos são mais fortemente afetados pela privação social do que fêmeas. Estes resultados são interpretados sob o contexto das diferenças entre gêneros na biologia reprodutiva de *C. jacchus*, caracterizada por competição entre fêmeas pela posição reprodutiva e tolerância entre machos. Pressões seletivas podem ter favorecido, então, uma ligação afiliativa ao grupo social mais intensa nos machos, a qual se refletiria nos altos níveis de estresse de machos sob privação social. Então, observa-se claramente, que o sexo, a idade e o contexto social podem influenciar a resposta individual a mudanças no ambiente social.

Palavras-chave: *Callithrix jacchus,* diferenças entre gêneros, resposta de estresse, cortisol.

INTRODUCTION

The formation of the pair bond in reproductive callitrichids normally occurs gradually over a number of weeks (Stevenson & Rylands, 1988). In *Callithrix*, in particular the common marmoset (*Callithrix jacchus*), the most frequent social interactions between the members of the reproductive pair include affiliative behaviors such as contact, proximity and allogrooming (Vogt *et al.*, 1978; Evans & Poole, 1983, 1984; Sutcliffe & Poole, 1984; Schaffner *et al*, 1995) and sexual behaviors such as mounts, copulations and attempts to copulate (Kendrick & Dixson, 1984).

Social and sexual behaviors appear to be more frequent during the initial phase of pairing in both *C. jacchus* and *Callithrix kuhli* (Evans, 1983; Rothe, 1975; Schaffner *et al.*, 1995, Sousa *et al.*, 1997), and the simultaneous arch-bristle reflects the formation of a successful breeding pair (Evans & Poole, 1983; Silva & Sousa, 1997). In most studies, males were the main initiators of grooming. However, in a few cases, especially when an early pregnancy occurs, females may be more active in both social and sexual interactions

(Silva & Sousa, 1997). Pair bonded females respond more aggressively towards intruder females than bonded males to intruder males (Araújo & Yamamoto, 1993).

When challenged by any physical or psychological stress, social primates will typically show an elevation in the levels of both both sympathetic catecholamines (epinephrine and norepinephrine) and glicocorticoids (cortisol). These hormones stimulate the physiological stress response (Lovallo & Thomas, 2000). While most interpretations refer to proximate causes (Troisi, 2001), an evolutionary approach should include ultimate causes, such as those which may determine individual (Lovallo & Thomas, 2000) and gender (Kirschbaum *et al.*, 1992) differences.

Mendoza (1991), for example, recorded different gender-based responses to environmental change in *Callicebus moloch* and *Saimiri sciureus*. In the monogamous *Callicebus*, the presence of the mate reduced cortisol levels in the context of an unfamiliar situation or novel object, whereas in *Saimiri*, which lives in large, mixed gender groups, the presence of a cage-mate had no effect. The “social buffering” (Cohen & Wills, 1985) observed in *Callicebus* may also occur between non-breeding individuals in callitrichids (e.g. Smith & French, 1997; Norcross & Newman, 1999). Studies of pair separation indicate that the loss of homeostatic regulatory mechanisms provide by the presence of social partners is a more important of increasing hormone levels than the isolation in itself.

In captive *C. jacchus*, changes in the social environment tend to be stressful, and trigger specific behavioral and hormonal responses, with different patterns in males and females, even for stressful events occurring during infancy (Dettling *et al.*, 2007; Pryce *et.al*, 2005) or juvenile and subadult stages (Silva, 2003). In fact, basal cortisol levels in males tend to be lower than those in females (Saltzmann *et al.*, 1994; Smith *et al.*, 1997; Raminelli, 2001), presumably reflecting the intolerance and competition among females with regard to reproductive status (Abbott, 1984; Saltzmann *et al*., 1996). The suppression of ovulation in subordinate females is well documented, but there are increasing records of selective polygyny and associated infanticides (Bezerra *et al*., 2007), all of which point to relatively high stress levels among females. Male tolerance appears to have been mediated, in particular, by the evolution of the callitrichid cooperative breeding system, which demands good fathers rather than competitive males.

In the present study, we explored these differences through experiments in social privation. In one approach, heterosexual pairs were separated and isolated, whereas in the other, same-sex subadult twins were removed from their family groups and isolated together. The differences found in both behavior patterns and hormone levels support the idea of differential selection pressures affecting the characteristics of the two sexes.

METHODS

Observation Conditions

The Primatology Nucleus at the Universidade Federal do Rio Grande do Norte (UFRN) in Natal houses a colony of *Callithrix jacchus* under natural local climatic conditions. Enclosures measure 2 x 2 x 1m, with lateral walls and galvanized wire front. A unidirectional mirror is located in the upper half of the back wall, which allows the discreet recording of behavioral data. Fecal samples were collected inside the cage by the observer immediately after defecation.

Experimental Procedure

Adult heterosexual pairs: For the analysis of the effects of separation on reproductive pairs, we used eight heterosexual pairs of adult *C. jacchus* (Table 1: C1-C8). All animals were captive born with the exception of male 691. The study was split in two phases:

Phase 1 (baseline): This phase starts when the subjects are removed from their home cages and placed together in a new cage. This phase lasted between 39 and 72 days;

Phase 2 (separation): The subjects were removed and placed alone in individual cages. This phase lasted seven or eight days.

Same-sex subadult twins: For the analysis of the effects of separation on same-sex twins, nine pairs of subadult subjects were selected (Table 1: M1-M5, F1-F4). Once again, the experimental procedure was divided into two phases:

Phase 1 (baseline): Subjects living in natal family group. This phase lasted between 48 to 72 days;

Phase 2 (separation): Twins were removed from the family group and house together in a new, unfamiliar cage. This phase lasted seven days.

Behavioral sampling

Observation sessions took place between 06:00 and 11:00 h. Data were collected in 30-minute focal-animal samples, collected three times a week for each pair during phase 1, and daily (heterosexual pairs) or three times a week (twins). When pairs of animals were observed, data were collected simultaneously for both subjects. In both cases (heterosexual pairs and twin couples) continuous recording was used. Behavior categories are described in Table 2. For heterosexual pairs, the data were collected between May, 1999, and January, 2001, whereas for the same-sex twins, the data was collected from March, 1999, to April, 2002.

Table 1. Pairings, age of the subjects and duration of experimental phases. Male (M) subjects are odd-numbered, females (F) are even-numbered. All same-sex pairs were twins.

Pair	Subjects	Age (months) at the start of the prodecure	Duration (days) of phase:	
			1	2
C1 (M-F)	579, 564	32, 29	48	8
C2 (M-F)	691, 612	Unknown, 22	72	8
C3 (M-F)	583, 468	23, 47	39	8
C4 (M-F)	521, 638	45, 21	47	8
C5 (M-F)	617, 598	33, 32	49	7
C6 (M-F)	659, 544	22, 38	57	7
C7 (M-F)	707, 654	17, 21	50	7
C8 (M-F)	559, 596	22, 18	39	7
M1 (M-M)	573, 575	12	48	7
M2 (M-M)	579, 581	11	72	7
M3 (M-M)	697, 699	9	63	7
M4 (M-M)	757, 759	9	63	7
M5 (M-M)	839, 841	10	58	7
F1 (F-F)	602, 604	10	51	7
F2 (F-F)	606, 608	7	49	7
F3 (F-F)	724, 726	11	55	7
F4 (F-F)	786, 788	9	53	7

Table 2: Description of behavioral categories (adapted from Saltzman *et al*., 1996).

Behavioral category	Description
Allogrooming	Use hands or mouth to pick through partner's fur
Autogrooming	Use hands or mouth to pick through its own fur
Piloerection	Arching posture with erection of the body and tail fur.
Scent-marking	Rub or drag anogenital region along substrate

Fecal collection and hormonal assays

Feces were collected twice a week during phase 1. In phase 2, feces were collected daily in reproductive pairs and twice weekly for twins. Cage floors were cleaned before sessions to facilitate detection of the feces, which were collected with disposable wooden spatulas. The material was placed in plastic tubes marked with the identity of the subject, time and date. Samples were then frozen at $^{-}20$ºC, until being assayed for cortisol.

Steroid extraction followed Ziegler *et al*., (1996). The enzymeimmunoassay (EIA) method for small samples (Munro & Stabenfeldt, 1984) was used to dose cortisol, using the alcoholic extracts produced by hydrolysis and etylacetate solvolysis, in 50 µl of each sample. Intra- and inter-assay coefficients of variation for cortisol were 3.06% and 6.09%, respectively.

Statistical analysis

Four behavior categories (autogrooming, allogrooming, piloerection and scent marking) were analyzed statistically, using either the frequency or the duration of events. As all behavioral variables had a normal distribution, it was possible to apply two-way ANOVA, Duncan's *post hoc* test and *t* tests to evaluate differences between males and females. In the case of the hormonal data, which were not distributed normally, values were transformed into natural logarithms (hormone +1), and Spearman's correlation coefficient was applied to the analysis of the relationship between behavior rates and hormone levels. All calculations were run in Statistic for Windows, 5.1.

RESULTS

Behavior Patterns

Autogrooming: In reproductive pairs, the mean duration of autogrooming bouts was significantly greater overall (combined phases) in females than in males (two-way ANOVA: $F = 14.04$, $p < 0.001$). While the duration of this behavior increased in both sexes during phase 2 (Figure 1A), there was no significant difference between phases or sexes.

In the twin dyads (Figure 1B), values were significantly higher for males in both phases (phase 1: $t = 20.47$, $p < 0.001$; phase 2: $t = 19.07$, $p < 0.001$). In addition, whereas the duration of bouts increasing significantly in males in phase 2 ($t = -2.28$, $p = 0.026$), no statistical difference was observed in female twins.

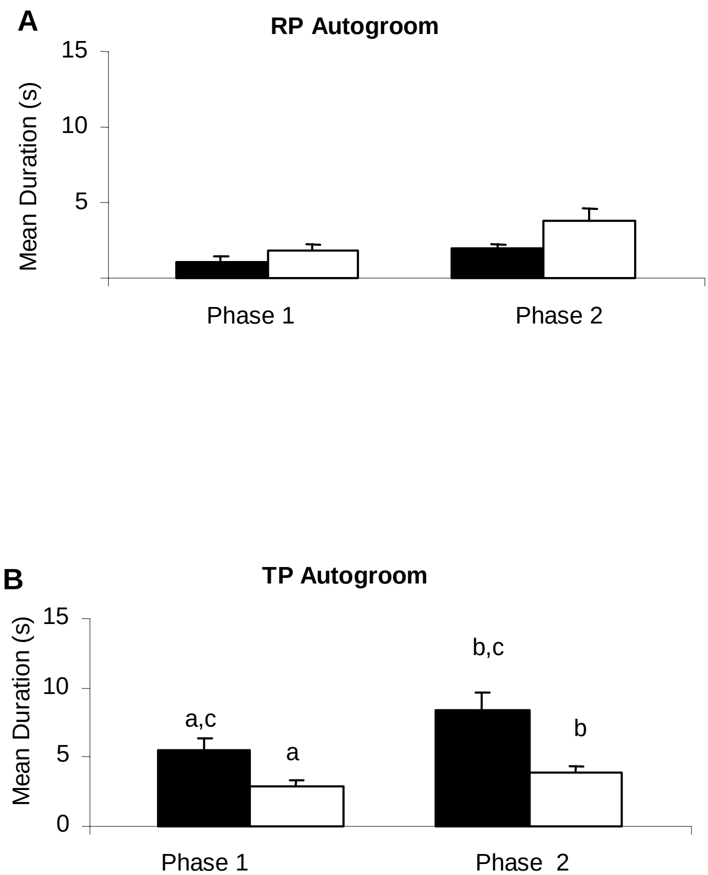

Figure 1. Mean (± standard error) duration of autogrooming bouts in: **A** male (black columns) and female (white columns) marmosets in heterosexual pairs; **B** male (black) and female (white) twin pairs [letters represent significant ($p <$ 0,05) differences (*t* test): (a) between males and females in phase 1; (b) between males and females in phase 2; (c) in males between phases].

Scent-marking: While males scent-marking slightly more than females in both phases in the heterosexual pairs (Figure 2A), no significant differences was found between sexes ($t = 0.76$, $p = 0.38$). In the twin dyads, by contrast, while there was little apparent difference between sexes in either phase (Figure 2B), marking rates increased significantly in phase 2 in both sexes (FF: $t = {}^{-}5.55$, $p < 0.001$; MM: $t = {}^{-}4.34$, $p < 0.001$).

Piloerection: In heterosexual pairs, piloerection was relatively frequent during phase 1 (Figure 3A), and declined significantly in phase 2 (FF: $t = 15.72$, $p < 0.001$; MM: $t = 10.20$, $p < 0.01$). Piloerection was also significantly more frequent in females than males during phase 1 ($t = 9.16$, $p < 0.003$). In twins, the behavior increased significantly ($t = -3.30$, $p < 0.001$) in males in phase 2 (Figure 3B), but not in females.

Allogrooming: Allogrooming bouts were of longer duration in male twins in comparison with female pairs (Figure 4). The difference between the sexes was significant in both phases, although the increase between phases was not significant in either sex.

Hormonal Patterns

In heterosexual pairs, cortisol levels increased in seven of the eight males in the two days following separation, but in only two of the females. Of the other females, three showed a decrease and three did not present any noticeable change in cortisol levels after separation. Cortisol levels increased, on average, for both sexes in each experimental condition (Table 3). In both cases, cortisol levels increased 3-4 times more in males than in females. In the case of the heterosexual pairs, there was a strong positive correlation ($r_s = 0.68$, n = 8, $p < 0.05$) between the time spent grooming in phase 1 and cortisol levels in phase 2, i.e. isolation appeared to be more stressful in animals that were more affiliative during the baseline period.

DISCUSSION

The results of the present study indicate that the age of the individual and the social context may modulate behavioral responses in *C. jacchus*. Social privation resulted in clear shifts in both behavior parameters and hormone levels, with distinct patterns in the two sexes.

Grooming behavior appeared to be more important in younger individuals than older ones, and the duration of events increased across the board under social privation.

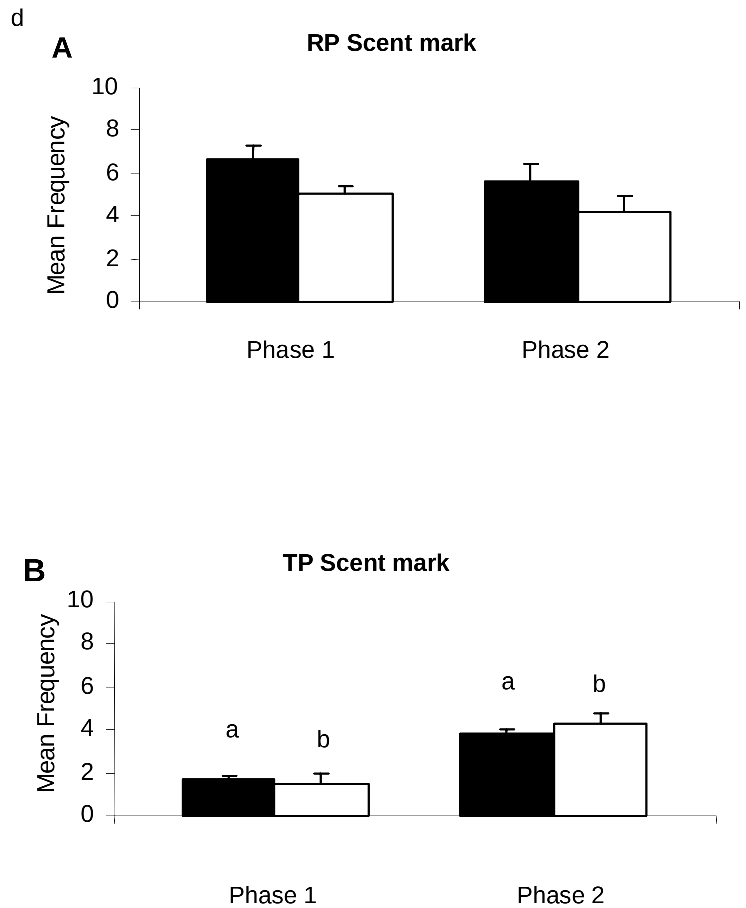

Figure 2. Mean (± standard error) frequency per observation session of scent marking in: **A** male (black) and female (white) marmosets in heterosexual pairs; **B** male (black) and female (white) twin pairs [letters represent significant (p < 0,05) differences (t test): (a) in males between phases; (b) in females between phases].

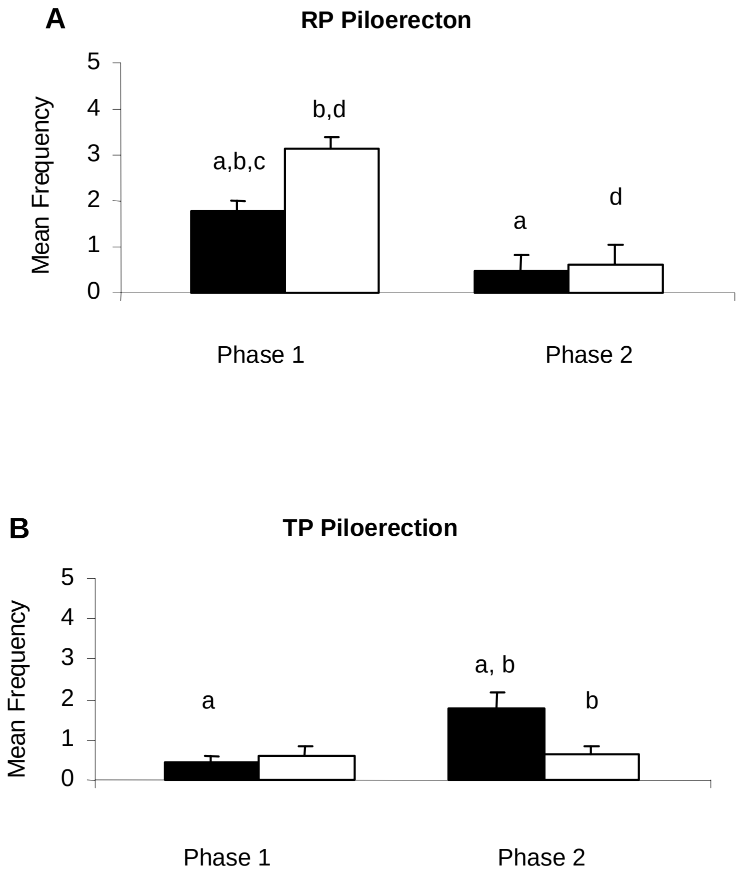

Figure 3. Mean (± standard error) frequency of piloerection in: **A** male (black) and female (white) marmosets in heterosexual pairs [letters represent significant (p < 0,05) differences (t test): (a) in males between phases; (b) between males and females in phase 1; (c) between males in phase 1 and females in phase 2; (d) in females between phases; (e) between females in phase 1 and females in phase 2]; **B** male (black) and female (white) twin pairs [letters represent significant (p < 0,05) differences (t test): (a) in males between phases; (b) between males and females in phase 2].

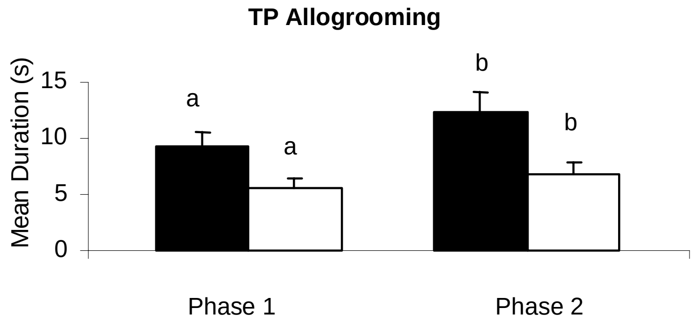

Figure 4. Mean (± standard error) duration of autogrooming bouts in same sex twins [letters represent significant (p < 0,05) differences (t test): (a) between males (black) and females (white) in phase 1; (b) between males and females in phase 2].

Table 3. Mean (± SE) fecal cortisol levels during phase 1 (baseline) and phase 2 (isolation) and mean percentage increase between phases. Mean values are based on cortisol levels recorded after four weeks in phase 1, and two days in phase 2.

Sex	Mean ± SE fecal cortisol (ng/g) in Phase 1 in: Heterosexual pairs	Mean ± SE fecal cortisol (ng/g) in Phase 1 in: Twins	Mean ± SE fecal cortisol (ng/g) in Phase 2 in: Heterosexual pairs	Mean ± SE fecal cortisol (ng/g) in Phase 2 in: Twins
Male	48.51 ± 16.65	46.54 ± 8.83	98.10 ± 46.77 (102.2%)[1]	67.42 ± 21.80 (44.(%)
Female	53.65 ± 23.79	59.60 ± 29.35	69.43 ± 27.05 (29.4%)	65.76 ± 20.53 (10.3%)

[1]Mean increase in comparison with Phase 1.

While there was no clear pattern in adults, immature males engaged in relatively long bouts of autogrooming, which increased significantly under privation. A similar pattern was recorded for allogrooming (Figure 4). A number of authors (e.g. Rothe, 1975; Woodcock, 1982; Evans & Poole, 1983) have identified males as “preferential” groomers, and this is reflected here.

Scent-marking behavior was less frequent overall in adults, but increased significantly under social privation, whereas it declined in immatures. This behavior is a clear sign of stress in adults (Epple, 1970; Saltzmann *et al*., 1994), primarily the female (Moura, 2001), and this was shown here.

Piloerection has important social functions, especially with regard to breeding behavior, and this is reflected in the results, in particular with regard to the high levels recorded in the adult females (Figure 3). High levels of piloerection are typical of newly paired marmosets (Evans & Poole, 1984; Silva & Sousa, 1995). Levels decreased significantly in adults of both sexes in the privation phase, clearly reflecting the lack of social context. The opposite pattern was observed in the twin pairs, in which the frequency increased significantly in the males under privation.

Privation resulted in increased cortisol levels in all groups, but the trend was more accentuated in males, both adult and subadult. While baseline levels may have been similar in the two sexes – reflecting fundamental mechanisms – females were less responsive, hormonally, to changes in the social environment.

The positive correlation between allogrooming and cortisol levels is similar to that recorded in *Callicebus moloch* (Mendoza & Mason, 1987), an obligatory monogamic species. The hormonal data presented here on *Callithrix jacchus* thus reinforce the link between hormones, social and behavioral parameters, in particular with regard to pair-bonding (see Evans & Poole, 1983; Kendrick & Dixson, 1983; Silva & Sousa, 1997),

Overall, the patterns observed in the present study appear to reflect ultimate causes molded by selective pressures, which have determined gender differences (Bradshaw, 2007). These differences presumably reflect the different social roles played by each sex in the reproductive process. Whereas females compete with other females for reproductive places, males are more affiliative, and may thus find social privation more stressful. This difference is less pronounced in immature individuals.

Recent studies developed in our laboratory reinforce the importance of taking gender differences into account in the study of stress responses in *C. jacchus*, as recorded in human beings (Blair, 2007). We have also shown consistent individual differences in stress reactivity at the population level, suggesting that this species is a suitable model for the study of both gender and individual differences in stress reactivity (Galvão-Coelho *et al.*, in press).

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