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RESEARCH ARTICLE

Crowding Increases Salivary Cortisol But Not Self-Directed Behavior in Captive Baboons

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Reduced space can lead to crowding in social animals. Crowding increases the risk of agonistic interactions that, in turn, may require additional physiological defensive coping mechanisms affecting health. To determine the stress induced from increased social density in a group of nineteen baboons living in an indoor/outdoor enclosure, saliva cortisol levels and rates of anxiety-related behavior were analyzed across two unique crowding episodes. Initially, mean salivary cortisol levels when animals were restricted to their indoor quarters were compared to those when they also had access to their larger outdoor enclosure. Then, mean cortisol levels were compared before, during, and after two distinct crowding periods of long and short duration. Crowding resulted in significantly elevated cortisol during crowding periods compared to non-crowded periods. Cortisol levels returned to baseline following two crowding episodes contrasting in their length and ambient climate conditions. These cortisol elevations indicate greater metabolic costs of maintaining homeostasis under social stress resulting from reduced space. Self-directed behavior, conversely, was not reliably elevated during crowding. Results suggest that the potential for negative social interactions, and/or the uncertainty associated with social threat can cause physiological stress responses detected by salivary cortisol. Self-directed behavioral measures of stress may constitute inadequate indicators of social stress in colony-housed monkeys or represent subjective emotional arousal unrelated to hypothalamic-pituitary adrenal axis activation. Am. J. Primatol. 77:462–467, 2015.

Key words: stress; salivary cortisol; crowding; anxiety; repetitive behavior; *Papio hamadryas hamadryas*

INTRODUCTION

Chronic stress is associated with myriad health concerns such as decreased androgen levels, neuronal cell death, decreased bone mineral density, gastric ulceration, and cognitive deficits [McEwen, 2007]. Physical and psychological stressors cause elevations in glucocorticoid hormones [Axelrod & Reisene, 1984]. Elevations in stress hormones are implicated in depression [Manji et al., 2001] and are known to impair adult hippocampal neurogenesis [Cameron & Gould, 1994]. Awareness of the causes and consequences of physical and psychosocial stressors is critical for garnering advances in the fields of stress-related disease [Chrousos & Gold, 1992] and animal welfare [Mormède et al., 2007].

Stress research in humans can utilize self-report of stress, however, this is not possible in animal models where behavioral measures are frequently used as proxies of negative emotion. Biological markers of altered homeostasis under threatening or emotionally charged situations that index an acute or sustained physiological stress response provide additional insight into the physiological, and perhaps, the disease-causing features of stress [McEwen, 2007]. Despite decades of productive stress research, much is still unknown about the interaction between threat, subjective emotional responses and stress-related endocrine markers.

Many non-human primate species possess complex social structures that engender frequent and severe stress. Thus, non-human primates provide a

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highly translational model to understand psychosocial stress responses [Sapolsky, 2005]. Studying stress responses that arise through conspecific interactions could be preferable to employing artificial stressors in characterizing species-typical stress reactions. Increased social density during crowding can increase aggressive interactions [Judge & de Waal, 1993]. The social uncertainty and vigilance under crowding can represent a potent stressor leading to elevations in stress-related behaviors and physiological reactions. Our aim was to simultaneously assess behavior and physiology in a large social group of captive baboons under disparate social stress conditions using non-invasive techniques. We evaluated crowding-induced variation in salivary cortisol, a glucocorticoid hormone of the hypothalamic-pituitary-adrenal axis (HPA-axis), since it is a validated metabolic stress marker. We also measured repetitive and self-directed behavior (SDB) considered as behavioral indicators of stress and anxiety in primates [Troisi, 2002]. We predicted that cortisol levels would increase in concert with self-directed repetitive behavior under crowding-induced psychosocial stress conditions.

METHODS

Subjects and Housing

A captive group of 19 socially-housed hamadryas baboons (*Papio hamadryas hamadryas*) ranging in age from infancy to 17 years was studied. Subject descriptions are provided in Table I. Subjects were housed in an indoor/outdoor enclosure measuring $9 \times 11 \times 4.5$ m for the outdoor portion with an adjacent $9 \times 6 \times 2.25$ m concrete, temperature-and humidity-controlled (22 ± 2 °C, 30–70%, respectively) indoor quarters divided into three compartments (diagram in Fig. 1A). The outdoor area was enclosed in chain-link fence and contained gravel and boulder substrate with various perches, large steel climbing structures, swings and multiple enrichment devices. Fruits, nuts, vegetables, grains and seeds were spread throughout the available enclosures daily. Enrichment devices such as rawhide, logs, plastic balls and bamboo branches were available in indoor and outdoor enclosure space year-round. Commercial primate diet (Mazuri Primate Browse Biscuits and L/S Banana Sticks) and fresh tap water were continuously available. Baboons were either non-crowded (had access to both indoor and outdoor areas or were restricted to the outdoor enclosure), or crowded (restricted to their indoor enclosure). Baboons underwent chronic long-term crowding each winter when the temperature fell below 7 °C and they were restricted to one or more of the three interconnected indoor compartments for several weeks. During the course of this study, monkeys also underwent an acute short-term crowding episode for four days when they were restricted to their indoor compartments while the outdoor enclosure underwent routine maintenance. Under these conditions, all of the baboons were housed as a single group. The only exceptions were when a single juvenile male was removed due to aggressive incompatibility with the alpha male harem leader and when a juvenile female was removed for treatment of bite injuries. Husbandry and experimental procedures were approved by the Bucknell University Institutional Animal Care and Use Committee in accordance with federal guidelines and conformed to the American Society of Primatology Principles for the Ethical Treatment of Primates.

Saliva Sample Collection and Cortisol Assay

Saliva samples were collected 2–3 times per week by multiple investigators sampling numerous baboons simultaneously using a previously described, non-invasive technique [Pearson et al., 2008]. Briefly, several experimenters held one or two pole apparatuses containing flavored cotton rope to willing baboon participants through an enclosure

TABLE I. Demographics of Subjects Sampled for Saliva

Subject ID	Sex	Age (years)	Ordinal rank	Samples	Mean cortisol
As	**M**	**1**	**9**	**5**	**20.82**
Ca	F	1	10	4	15.06
Ch	**M**	**4**	**6**	**58**	**15.91**
Cr	**M**	**3**	**6**	**52**	**19.46**
Ka	**F**	**4**	**5**	**46**	**21.42**
Kb	**M**	**6**	**2**	**64**	**17.36**
Kr	**M**	**5**	**4**	**48**	**13.59**
Rb	**F**	**4**	**5**	**59**	**15.48**
Rh*	F	2	7	34	20.47
Ro	**M**	**5**	**4**	**58**	**15.93**

Indicated are the subset of baboons that provided saliva samples. Subjects in bold met criteria to be included in behavioral and salivary analyses. Samples refers to the number of saliva samples analyzed per subject with EIA. Two subjects (*), despite providing numerous saliva samples, were excluded for the following reasons: Cl - young adult male commonly separated indoors from other subjects due to severe fighting with the dominant harem leader Dg; Rh—juvenile female baboon received veterinary intervention to treat injuries resulting from bites during herding by adolescent Kr. Unit of measurement for mean cortisol is ng/ml.

TABLE II. Self-Directed Behavior Categories Collected During Focal Observations

Behavior	Definition
Scratch	Repeated movements of the hand or foot during which the fingers/fingernails or toes/toenails were drawn across the fur or skin at least three times. Bouts of scratching ended with interruptions of more than five seconds.
Self groom	Picking through and/or slowly brushing aside fur with hands and/or mouth for at least five seconds. Self groom included picking at wounds and ended with interruptions of more than ten seconds.
Shake	Subject performed a reciprocating tremble of their entire body.
Self touch	Body contact with the hand: included wiping eyes, inspecting feet, and placing hand to mouth. Instances of Scratch or Self groom that did not meet the time or frequency requirement were recorded as self touch.

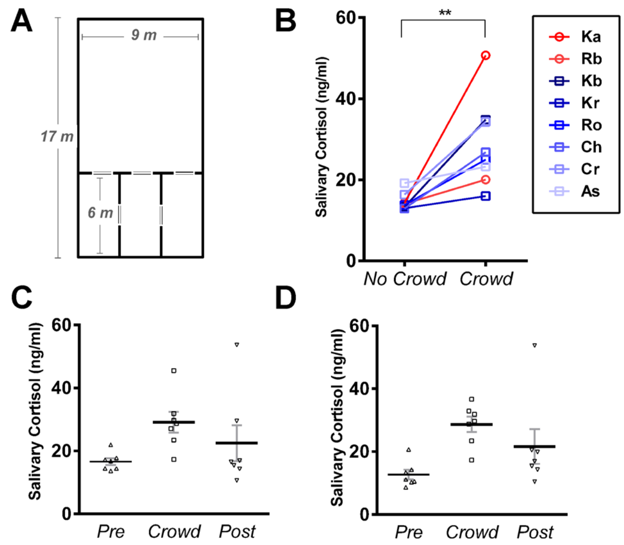

Fig. 1. Crowding causes elevation in salivary cortisol. Overhead diagram of baboon enclosure depicting the outdoor section and three interconnected indoor chambers (A). Independent of climate conditions mean cortisol levels per subject were higher during indoor restriction (Crowd) compared to non-crowded housing (B). The legend lists subject identifiers; square symbols represent male monkeys while circles represent females and darker shades correspond to older individuals (range ~ 1–6 years old). Cortisol levels were elevated when Crowded compared to matched samples collected prior to (Pre) or after (Post) crowding (B,C). Cortisol was elevated during a chronic winter crowding period (B), and during an acute four days of crowding when the weather was not cold (C). Figures 1B and 1C depict the mean average cortisol level for each subject as well as Mean ± 1 SEM across subjects.

fence or gate. A single saliva sample was collected from multiple monkeys at a time (from 2–8 animals per session). All sampling sessions were performed at the same time in the diurnal cycle (~1300 hr). Saliva samples (~300 ul/sample) were aliquoted and frozen at −80 °C until analyzed with a commercial cortisol enzyme-immunoassay (EIA) kit (Cayman Chemicals, Ann Arbor, MI) previously validated for baboon saliva [Pearson et al., 2008]. Obtained Mean (± SEM) intra-assay and inter-assay coefficients of variation were 6.62 ± 0.35% and 5.57 ± 0.49%, respectively. Salivary cortisol levels were measured as nanograms per milliliter (ng/ml) saliva.

Behavioral Observations

Focal behavioral observations were conducted regularly throughout all housing arrangements between 0900 and 1700 hr. Focal observations lasted 10 min and were conducted on all baboons in the colony 3–5 times a week. The focal subject was determined randomly using a random number generator. Self-directed behavior categories collected were scratch, self-groom, shake and self-touch and their definitions are listed in Table II. Observations were collected by one of four investigators demonstrating inter-observer reliability greater than 90% (percent agreement).

Experimental Design and Statistical Analyses

To determine if crowding altered circulating cortisol levels, two analyses were conducted: 1: a Binary Crowding Analysis, where monkeys were either crowded or not, and 2: a Quadratic Analysis where values were compared prior to, during and after crowding in a matched manner. For the Binary Crowding Analysis, cortisol values were averaged within each Housing Condition to provide a composite mean, per subject, per period. Thus, the mean average level of cortisol samples collected during non-crowded conditions (when the baboons had outdoor access) was compared to the mean of the per-subject averages during crowding (restricted indoors) with a Wilcoxon matched-pairs signed rank test for the baboons that reliably provided saliva samples. For the Quadratic Analysis mean salivary cortisol levels were compared before, during and after restriction to the smaller indoor enclosure during a single winter (~7 weeks indoors) as well as during a brief, four-day period in the Fall using Friedman tests with Dunn's multiple comparisons. Non-parametric tests were selected due to unequal variances between conditions. We predicted that cortisol levels would be higher during crowding, and that in the latter analyses, cortisol would be lower during pre- and post-crowding intervals. To be included in analyses, baboons needed to provide at least two saliva samples per period for each crowding sample.

Rates of self-directed behavior were also calculated for the same crowding periods analyzed for the cortisol crowding comparisons (Quadratic Analysis) for eight young baboons. At least two 10-min focal observations were compared for each subject during each housing phase. Mean rate of each of the four self-directed behavioral responses was calculated for each subject (expressed in frequency per ten minutes) and compared before, during and after crowding periods. For behavioral comparisons, parametric tests were conducted since variances were similar across conditions. GraphPad Prism (V6.0) and SPSS (V21) were used for statistical comparisons.

RESULTS

Eight of the young baboons were included in cortisol and behavior analyses as they reliably provided saliva samples throughout the study (Table I). Adult and subadult baboons were largely disinterested in participating or were isolated from the group due to aggression. These animals were excluded from analyses in order to prevent few samples or social isolation from skewing the results.

Binary Crowding Analysis

The average of each baboon's mean cortisol level from all samples collected during crowding was significantly higher than the average of the sample means from each subject during periods of access to outdoor enclosure space ($P < 0.01$, $n = 8$ Fig. 1B).

Quadratic Analysis

Mean cortisol levels during the chronic crowding period and during an acute crowding period were compared to an equal number of samples from each subject collected in the period immediately before and after the respective crowding housing arrangement. Seven baboons provided at least two saliva samples in each of the conditions and were included. During the chronic crowding period, mean salivary cortisol levels significantly differed ($P < 0.05$, $n = 7$), indicating elevated cortisol during crowding (Fig. 1C). Post-hoc analyses indicated that the pre-crowding cortisol levels were significantly lower than the crowding levels ($P < 0.05$) and the post-crowding samples were significantly lower than the crowding ($P < 0.05$). Likewise, during the acute crowding period of four days when the weather was not inclement, the mean cortisol levels were significantly different across the three conditions ($P < 0.01$, $n = 7$) and post-hoc tests indicated that the pre-crowding cortisol levels were significantly lower than crowded levels ($P < 0.01$). The comparison of post-crowded to crowded cortisol levels was not significant.

Self-Directed Behavior

One way repeated measures ANOVA for each of four categories of SDB showed no significant alterations for self-directed behavior samples collected during crowding and compared to matched samples collected prior to and following crowding in either crowding period (Table III).

DISCUSSION

Using focal behavioral quantification techniques and a validated salivary cortisol assay, we explored whether stress variables were modulated by social density in young members of a captive baboon colony. We found a robust elevation of cortisol in baboons during crowding conditions (when housed in temperature-controlled but crowded conditions) and during an independent period when monkeys were temporarily crowded indoors but not due to cold weather (Mean $\pm$ 1 S.E.M. high temperature was 14.9 ± 1.33 °C).

Crowding-induced elevations in cortisol have been documented in gerbils [Hull et al., 1976] laboratory mice [Fullwood et al., 1998] and rats [Brown & Grunberg, 1995]. Elevated hair cortisol has been detected in rhesus monkeys as a function of social density [Dettmer et al., 2014]. However, chimpanzees restricted to indoor quarters for two days during a hurricane did not display elevated urinary cortisol [Anestis, 2009]. An early study [Sassenrath, 1970] demonstrated covarying elevations in ACTH and anxiety-related behaviors in captive rhesus monkeys during socially threatening conditions. Although the literature on the effect of crowding on

TABLE III. Quadratic Comparison of Self-Directed Behavior (SDB) Across Two Crowding Events

	Winter, chronic crowding				Fall, acute crowding			
	Pre	Crowd	Post	*P*-value	Pre	Crowd	Post	*P*-value
Scratch	2.21±0.28	1.94±0.47	2.21±0.45	0.87	2.56±0.34	1.72±0.67	2.00±0.52	0.48
Self Groom	0.50±0.13	0.81±0.15	0.44±0.14	0.27	0.43±0.06	0.29±0.11	0.33±0.09	0.27
Shake	0.23±0.08	0.13±0.04	0.17±0.04	0.45	0.07±0.01	0.05±0.02	0.06±0.01	0.55
Self Touch	1.92±0.3	1.63±0.35	1.92±0.37	0.71	1.61±0.42	1.17±0.26	2.61±0.68	0.14
Combined	4.85±0.52	4.50±0.89	4.73±0.92	0.94	4.66±0.53	3.22±0.91	5.00±1.17	0.39

Mean $\pm$ 1 S.E.M. rates of self-directed behavior were not significantly different during crowding as compared to equal observation periods before and after crowding. Combined rates across SDB categories also failed to reach statistically significant differences.

glucocorticoids in captive mammals appears incongruous, the variety of methodologies utilized and the types of social systems and threat scenarios might underlie the variability of results. The current study provided novel evidence that crowding can lead to elevated glucocorticoid levels in primates, albeit in a subset of baboons that does not represent the entire age range of monkeys in the colony.

Given the complexity of threat scenarios and the subtle alterations in psychological anticipation of social stressors, behavioral indicators might provide useful measures of social stress [Pearson et al., 2011]. [Judge & de Waal, 1993] found that pacing, an ostensible indicator of stress or anxiety increased under short-term crowding in rhesus macaques (*Macaca mulatta*). Given elevation during threat, self-directed behavior (SDB) has been proposed as a reliable indicator of stress and emotional arousal [Maestripieri et al., 1992]. We predicted that monkeys would display robust elevations in rates of SDB while crowded alongside elevations in cortisol. Our results did not support this prediction and endorse other studies demonstrating a lack of a positive relationship between SDB and cortisol in a captive orangutan [Elder & Menzel, 2001] and in wild baboons [Ellis et al., 2011; Higham et al., 2009]. Cortisol levels in captive monkeys can show a negative relationship with more severe forms of SDB such as self-injurious behavior [Tiefenbacher et al., 2000]. Children diagnosed with autism spectrum disorder that show higher repetitive behaviors display lower levels of cortisol [Gabriels et al., 2013]. Taken together, the current study, when placed into context with existing literature, indicates that multiple stress indicators might be required to identify the influence of social stress in animals and an assumption that SDB predicts HPA-axis activation is erroneous. The behavioral and physiological discordance in this study advocate caution and appreciation of the complexity of stress and its diverse psychological and biological parameters.

The current approach benefited from simultaneous sampling across multiple monkeys and attempted to avoid confounding circannual influences [e.g., Schiml et al., 1999] on cortisol-spatial density relationships. A limitation of the current study was that the behavioral parameters were not collected in a matched manner to correspond to saliva collection. Ideally, one could track salivary cortisol levels in real-time and in coordination with behavioral observation to assess covarying cortisol and SDB. This is likely not possible in unrestrained monkeys.

Dettmer and colleagues [2014] claimed that sampling techniques that reflect chronic cortisol levels (i.e., hair) are preferential to acute samples such as plasma or saliva to reflect chronic stress. Our approach utilized saliva that provided acute cortisol levels. We argue the average of numerous acute samples can provide a valid index of both acute and chronic cortisol levels. In any case, behavior-physiology relationships will require large sample sizes given their respective extents of variability. Taken together, and given the reliable increase in cortisol during crowding in the absence of behavioral stress indicators of the current study, SDB variables may reflect acute emotional responses whereas circulating glucocorticoid elevations require diffuse and sustained arousal from severe social threat. Another possibility is that crowded monkeys employ conflict reduction strategies to reduce social uncertainty and aggression, which in turn reduces self-directed activity. Under social threat, enhanced vigilance, appeasement signals and affiliation [Judge et al., 2006; Judge & de Waal, 1997] might reduce uncertainty more than SDB. Future experiments could evaluate the coordinate investment in these mutually exclusive behaviors under varying social densities or in periods of social unrest in captive monkeys.

The goal of the study was to evaluate ongoing stress levels in animals minimally influenced by the experimenters. The limitation of this experimental design arises from the voluntarily nature of saliva sampling. Consequently, salivary cortisol levels were not representative of the colony composition and mainly came from juvenile monkeys. The specific temperaments and life stage of the monkeys could limit the generalizability of the findings. Nevertheless, this study provides evidence that crowding is stressful as measured by cortisol, and the variable recovers after removing the stressful context. This effect is not reliably revealed by common behavioral measures.

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