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NEWS AND PERSPECTIVES

Hormonal changes in northern white-cheeked gibbons (*Nomascus leucogenys*) after the death of a group member

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Abstract

The small apes, gibbons and siamangs, are monogamous species with their social groups comprising of both parents and their offspring. Therefore, the loss of a member may elicit a stress response in the remaining members due to their strong bonds. Glucocorticoids (GCs) have been useful indicators of stress, but distinguishing between acute versus chronic stress may be limited when measuring these hormones alone. The adrenal hormone dehydroepiandrosterone-sulfate (DHEAS), a GC antagonist, has been implicated in the regulation of the stress response. Thus, the concomitant measurement of these hormones can help examine whether an event, such as the loss of a group member, elicited a stress response. In this brief report, we discuss the hormonal response of two zoo-housed northern white-cheeked gibbons (*Nomascus leucogenys*) (1 adolescent male and his mother) after the death of the adult male of the group. Baseline fecal samples were collected opportunistically from these two individuals 5 months prior, and 3 months following the death of their group member. A total of 25 samples were quantified for fecal GC metabolites (FGCMs) and DHEAS by enzyme immunoassay (EIA) to calculate the FGCMs:DHEAS ratio. Our results indicate an increase in FGCMs and FGCMs:DHEAS for the adolescent male, but not the adult female, following the death. Our findings suggest that the integration of FGCMs and DHEAS measurements can provide valuable information to interpret individual stress levels to the sudden change in the group's social structure.

Keywords Death · Gibbons · Group structure · Glucocorticoids · DHEAS · Stress

Introduction

The study of death in non-human primates is limited due to its sudden aspect in wild populations and removal/euthanasia in captive populations. Regardless, behavioral responses to the death of a group member have been documented in primate species including marmosets (*Callithrix jacchus*) (Bezerra et al. 2014), macaques (*Macaca spp.*) (Sugiyama et al. 2009; Campbell et al. 2016; Minami and Ishikawa 2023; Arlet et al. 2023), baboons (*Papio hamadryas ursinus*) (Engh et al. 2006), geladas (*Theropithecus gelada*) (Fashing et al. 2011), orangutans (*Pongo abelii*) (Dellatore et al. 2009), and chimpanzees (*Pan troglodytes*) (Biro et al. 2010; Anderson 2018). While most of these studies focus on dead-infant carrying behavior (Sugiyama et al. 2009; Dellatore et al. 2009; Biro et al. 2010; Fashing et al. 2011; Li et al. 2012; Takeshita et al. 2020; De Marco et al. 2022; Arlet et al. 2023), death occurrences outside of the mother–infant bond are less common (Engh et al. 2006; Buhl et al. 2012; Bezerra et al. 2014; Campbell et al. 2016; De Marco et al. 2020, 2022; Minami and Ishikawa 2023). Moreover, the study of stress hormones in relation to death is limited in non-human primate studies, because it requires sample collection from subjects before they witness death of a conspecific.

Stress, either physical or psychological, results in the activation of the hypothalamic–pituitary–adrenal (HPA) axis which results in a cascade of hormonal release that culminates with secretion of glucocorticoids (GCs) from the adrenal gland (Selye 1971). A prolonged state of heightened GC secretion can lead to detrimental effects, such as decreased immune response, impaired cognitive function, and, in some cases, adrenal fatigue that can lead to lowered GC levels (Fraser et al. 1999; Cleare et al. 2001; Žarković

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et al. 2003; Lennartsson et al. 2015; Kamin and Kertes 2017; Pawluski et al. 2017). As a result of adrenal fatigue, lowered GC levels during chronic stress can be misconstrued as low stress. Therefore, the concomitant measurement of GC antagonists, such as dehydroepiandrosterone (DHEA) or its sulfated form DHEAS, can avoid potential misinterpretations (Whitham et al. 2020). Due to the competitive nature of these hormones, the ratio of GCs to DHEAS can help to distinguish acute stress (low GCs:DHEAS or temporary high GCs:DHEAS) from detrimental, chronic stress (sustained high GCs:DHEAS), which is critical for monitoring animal welfare (Whitham et al. 2020). In humans, distress or depression has been associated with elevated cortisol (Irwin et al. 1988) and high GCs:DHEAS ratio (Goodyer et al. 1998; Grillon et al. 2006; Vitlic et al. 2014). This disruption in the balance of these adrenal hormones is associated with decreased immune function in humans (Khanfer et al. 2011) and rhesus macaques (*M. mulatta*) (Rais et al. 2017), increased rates of depression (Goodyer et al. 1998, Goncharova et al. 2010), and increased neurotoxicity (Kimonides et al. 1999) and could therefore be useful to detect psychological stress in non-human primates. In this context, the use of hormones in comparative thanatology of our closest living relatives may provide further context of an individual's response to the death or loss of a group member.

The purpose of this research was to evaluate the stress response of two gibbons, an adult female and her adolescent male offspring, in the months following the removal and subsequent euthanasia of their partner and father, respectively, through fecal steroid measurements. We tested whether fecal glucocorticoid metabolite (FGCM) levels increase following the loss of a group member and whether the behavioral changes noted by the animal care team corresponded with high FGCMs:DHEAS ratio in the two surviving members of the group.

Methods

Study subjects

The subjects in the current study were a mother–offspring pair of northern white-cheeked gibbons (*Nomascus leucogenys*). The subjects were housed at a zoological facility in the United States. The adult male and female were paired in August 1995 and successfully reared 4 offspring including the adolescent male in the present study. Two of the offspring were present in the family when the adolescent male was born. At the time of the adult male's death, the adolescent male was the only offspring present. The adult female was 32 years old, while the adolescent was 6 years old at the start of this study. The adult male gibbon was 35 years old at the time of his death. Additionally, the female was the primary social play partner for the adolescent male.

Data collection

The adult male died suddenly in September 2020. Before his death, the adult male was lethargic and limited in his movements. Animal care staff anesthetized the male in the night enclosure, which is hidden from public view, to be taken to the animal hospital for evaluation and subsequent euthanasia. During this process, the adult female and adolescent male were on exhibit. Behavioral data and fecal samples were collected non-systematically (ad libitum) by the animal care staff due to the sudden death of the adult male (and lack of staff to monitor the animals for long periods due to the COVID-19 pandemic) until the end of the sample collection period.

Animal care staff collected fecal samples opportunistically during daily husbandry and stored the samples in bags labeled with ID and time of collection in freezers (– 20 °C) on site. Samples were collected from the adult female and adolescent male prior to the adult male's sudden death as part of an unrelated research project. These baseline samples ($N = 3$/individual) were collected for 1 week, 5 months prior to the male's death for a total of 6 samples. After the loss of the adult male, three samples were collected every 4–5 weeks for 3 months for the female ($N = 9$) and the adolescent male ($N = 10$), for a total of 19 samples post-death.

Feces extraction

We followed the fecal extraction methods reported in Takeshita (2022) for the measurement of both DHEAS and FGCMs. Briefly, we lyophilized the samples using a freeze dryer (cat #700,201,000, FreeZone, Labconco). Next, we pulverized the samples and sifted out extraneous materials. Then, we added 5 mL of 80% methanol to approximately 0.1 g of feces (mean ± SD = 0.104 ± 0.01). We then vortexed the samples for 30 min to homogenize the samples followed by centrifugation (3000 rpm × 10 min). After centrifugation, we removed the supernatant (2 mL) from each sample. An aliquot of 500 µl was dried down under nitrogen and stored at -20 °C until they were assayed by enzyme immunoassay (EIA).

Steroid analyses

The DHEAS assay has been developed, described, and validated in hylobatids (Takeshita 2022). We calculated the intra-assay coefficient of variation (CV) as the mean CV obtained from duplicate samples (4.44%, $N = 25$). We analyzed FGCMs with an 11-oxoetiocholanolone EIA, previously described (Palme and Möstl 1997). This EIA measures

11,17-dioxoandrostanes, a group of fecal cortisol metabolites. Intra-assay CV was 1.23%. All samples were assayed on one plate per steroid. Steroid concentrations were calculated as nanograms per gram of dry feces.

Biological validation of the FGCMs assay was conducted opportunistically based one male gibbon (*N. leucogenys*) from a different zoological facility which had fallen approximately 10 m from a rope in his enclosure (see Takeshita 2022 for more details). We collected daily samples from this individual, starting 3 days before the accident, the morning before the accident (Day 0), and days 1 and 3 following the event ($N=6$). To determine which of the samples post-stress was considered an FGCMs peak as indicative of a stress response, we used an iterative process to determine baseline FGCM levels (Brown et al. 1999, 1994; Heintz et al. 2011). Briefly, we calculated the mean hormonal levels using initially all 6 samples from this case. Any sample above the mean ± 1.5 standard deviation (SD) was temporarily removed as an outlier, and the mean was recalculated. This process was repeated until all samples fell within the mean ± 1.5 SD range (Heintz et al. 2011). Then, all 6 samples were plotted, and any sample above the baseline (mean ± 1.5 SD) was considered a peak (Supplementary Fig. S1a). In comparison to the baseline mean, the stress event resulted in a threefold increase in FGCM levels 1 day after the stressor (Supplementary Fig. S1a), and FGCM levels fell within baseline ± 1.5 SD levels within 3 days after the stressor. This response indicates that our assay was adequate for measuring FGCMs from feces in this species. The FGCMs:DHEAS ratio remained within baseline levels (Supplementary Fig. S1c).

Descriptive statistics

Due to the small sample size, statistical analyses were not performed in the present study. Therefore, descriptive statistics showing the monthly means and SDs were used to demonstrate the hormonal patterns. We used the raw data to calculate monthly averages of FGCM levels, fecal DHEAS levels, and FGCMs:DHEAS ratio. To determine the response to the loss of a group member, samples measured prior to the death were identified as baseline levels for the purpose of this study and averages (mean value ± 1.5 SD) were calculated per individual for each hormonal index (FGCMs, fecal DHEAS, and FGCMs:DHEAS ratio).

Results

Behavioral observations

According to the animal care staff, vocalization patterns of the adult female and adolescent male changed after the death. The adult female used to begin the territorial calls but after the adult male's death, the staff noticed that the adolescent male started to initiate these calls. Additionally, the pair was not as active in their night room, but in the presence of visitors, their behavior appeared normal. The adult female and adolescent male were also more resistant to separation by the animal care staff.

Steroid analysis

Baseline FGCM levels for the adult female and adolescent male were 95.0 ± 30.9 ng/g and 264.8 ± 63.85 ng/g (mean ± SD), respectively. Baseline fecal DHEAS levels were 2963 ± 392 ng/g and 5636 ± 408 ng/g. After the death, there was a steep increase in FGCM and fecal DHEAS levels for the adolescent male with FGCM levels three times (900 ± 201 ng/g) and fecal DHEAS levels nearly twice (9560 ± 2588 ng/g) as high as baseline in the second month post-death. FGCM and fecal DHEAS levels decreased within the third month. Meanwhile, the adult female maintained similar FGCM and fecal DHEAS levels throughout the study with no pronounced increase beyond baseline levels after the adult male's death (Fig. 1a, b).

Baseline FGCMs:DHEAS levels for the adult female and adolescent male were 0.03 ± 0.01 and 0.05 ± 0.01, respectively. After the death of the adult male, the adolescent male had a sustained, elevated FGCMs:DHEAS ratio that was above baseline for 2 months (Month 1 = 0.07 ± 0.02; Month 2 = 0.08 ± 0.01), which decreased to baseline in the third month (Fig. 1c). Conversely, the FGCMs:DHEAS ratio of the adult female maintained similar levels throughout the sample collection period.

Discussion

We observed different adrenal secretion pattern between the individuals in the months after the death of the adult male. The adolescent male exhibited sustained elevated FGCMs:DHEAS during this time, while hormone levels in the adult female remained within baseline levels. In the acute stress event reported here (fall from a rope, Supplementary Fig. S1), the gibbon's FGCM levels increased above baseline range the day after the stress event and returned within 3 days post-stress. In contrast, the FGCMs:DHEAS ratio remained within baseline levels, indicating that both fecal DHEAS and FGCMs responded to the stressor immediately until the stress was no longer perceived. This pattern is typical of acute stress, whereas chronic stress can be characterized by sustained elevated GC:DHEAS ratio (Moriguchi Jeckel et al. 2010; Lennartsson et al. 2013).

The increase in FGCMs:DHEAS ratio in the adolescent male following the death of his father is suggestive of

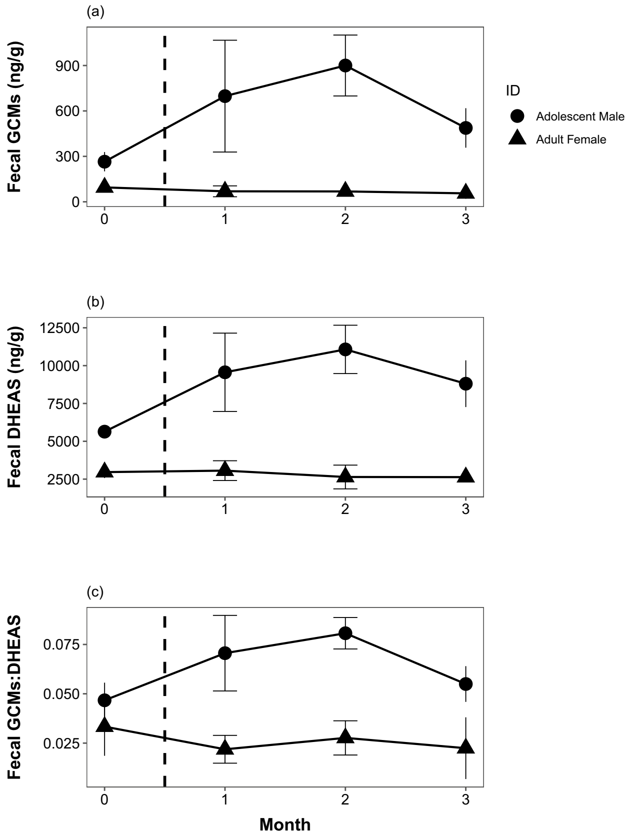

Fig. 1 Monthly mean concentrations of **a** fecal GCMs, **b** fecal DHEAS, and **c** the fecal GCMs:DHEAS ratio of a zoo-housed adolescent male (triangle) and an adult female (circle) northern white-cheeked gibbon before (month = 0) and after (months 1–3) the death of an adult male (indicated by the vertical dashed line. Error bars represent the SD

overactivation of the HPA axis, consistent with chronic stress (Grillon et al. 2006; Moriguchi Jeckel et al. 2010; Lennartsson et al. 2013). Sustained elevated GCMs:DHEAS has been identified in bereaved elderly adults (Khanfer et al. 2011) and adolescents exhibiting depressive behaviors (Goodyer et al. 1998). In this study, both individuals had behavioral changes after the death of the family member. However, while the adolescent male had elevated FGCMs:DHEAS during the 3 months, this study did not capture an adrenal response in the female reflective of stress to the loss of her companion. This difference could be due to the different relationships the gibbons had to the deceased. In a study measuring GC levels in female chacma baboons, females who lost close relatives to predation had significantly higher GC levels than females that did not despite all females being in the presence of the attacks (Engh et al. 2006). Interestingly, the related females' GC levels returned to baseline within 2 months of the death. Behavioral observations, such as increased grooming, supported the physiological results measured by the researchers (Engh et al. 2006). Similarly, a study in humans reported that grieving humans with higher social support had lower GC:DHEAS ratios (Vitlic et al. 2014). In the present study, both gibbons maintained proximity during the sampling period, which could have mitigated stress in the female, but not in the adolescent male, suggesting that kin relationship might also affect how gibbons cope with the death of a group member.

Despite their monogamous bonds, direct paternal care is not commonly observed in gibbons as it is in other monogamous primate species such as owl monkeys (*Aotus spp.*) (Rotundo et al. 2005; Fernandez-Duque et al. 2008), callitrichids (Kleiman 1977), titi monkeys (*Callicebus cupreus*) (Schradin et al. 2003), fat-tailed dwarf lemurs (*Cheirogaleus medius*) (Fietz 1999), and siamangs (*Symphalangus syndactylus*) (Chivers 1974; Lappan 2005). However, during the juvenile period, the gibbon father enforces his social role by supervising, or "babysitting" the offspring as they learn independence and to interact socially in the absence of other subadult gibbons (Chivers 1974; Lappan 2005; Whittaker and Lappan 2009; Rafacz et al. 2012). Researchers suggest that this "babysitting" strategy may be beneficial to the infant in that it encourages independency while reducing the frequency of more direct, but energetically costly, care behaviors such as carrying (Lappan 2009). In addition, in a gibbon group where no other subadult individuals were present, both parents were observed engaging in play behavior with their offspring (Brockelman et al. 1998). Thus, it is possible that the bonds between father and offspring were heightened by the absence of other group members. Further research into the pair-bond and paternal–infant bonds in gibbon populations are warranted.

While studies on ape attachment are limited, early studies on primate separation showed that young monkeys would exhibit increased vocalizations, agitated activity, postural changes, and reduced exploratory behavior when separated from their mothers (rhesus macaques: Harlow and Suomi 1974; squirrel monkeys (*Saimiri sciureus*): Hennessy 1986; Anderson 2016, 2017). Considering that these behaviors have been associated with sustained, elevated GCM:DHEAS levels (Goodyer et al. 1998; Grillon et al. 2006; Vitlic et al. 2014), the stress response observed through behavior and physiological measures in the adolescent male in the present study could have also been elicited due to the absence of a social partner.

In contrast, the lack of a physiological response in the female to the loss of her long-term partner could be indicative of a weaker bond between male and female northern white-cheeked gibbons. Previous research has identified extra-pair copulations in gibbons (Fan et al. 2006; Huang et al. 2013) and siamangs (Lappan 2007; Morino 2016), suggesting that their bond is not as strong as in other pair-bonded species, such as owl monkeys or titi monkeys (Schradin et al. 2003). Additionally, a study comparing pair-bond behavior in wild siamangs and white-handed gibbons (*Hylobates lar*) found that gibbon females contribute less to relationship maintenance (Palombit 1996). Palombit (1996) further suggests that, at least in this gibbon species, females may be slightly dominant to males. Alternatively, it is possible that our analyses missed the female's stress response due to our sampling timing, which began approximately 1 month post-death. Nonetheless, this would suggest that the female's hormonal response was shorter compared to the sustained elevation in adrenal hormones observed in the adolescent male. If this is the case, we hypothesize that increased proximity with the adolescent male functions as a stress mitigator for the female, which is similar to a case observed in chacma baboons (Engh et al. 2006).

An alternative hypothesis to the hormonal changes in the adolescent male but not the adult female could be due to the change in social status of the male. Gibbon pairs are commonly viewed as co-dominant, with low inter-sexual aggression and high inter-sexual grooming (Carpenter 1940; Barelli et al. 2008, 2011). Thus, it is possible that without the adult male present in the group, the increased adrenal response in the adolescent male was due to his sudden elevation in social status coupled with increased territorial behavior (i.e., territorial calls). Dominance in non-human primates is frequently associated with elevated GC levels (Muller and Wrangham 2004; Cavigelli and Caruso 2015; Takeshita et al. 2018). Additionally, dominance-related stress is expected to be higher during periods of rank instability (Sapolsky 1992). In the present study, although the change in rank was not a result of aggressive behavior, it may have resulted in a change in hormonal levels.

Interestingly, the animal care team observed that both gibbons were hesitant to move to their night room. Presumably, the two gibbons were aware of the ailing adult male's removal from this space. This hesitancy to move to the night room could be evident of avoiding a space associated with death or immobilization as has been observed in other ape species such as chimpanzees (Anderson et al. 2010) and gorillas (King 2013). In a well-documented case of death in captive chimpanzees, an adult female died in their night room on a bed of straw (Anderson et al. 2010; Anderson 2017). The surviving chimpanzees in the troop exhibited subdued behavior as they observed the caretakers remove the body of the deceased female (Anderson et al. 2010; Anderson 2017). Despite cleaning their night room, the chimpanzees were hesitant to return to their indoor quarters where the female died (Anderson et al. 2010; Anderson 2017). If these gibbons associated the night room with death or immobilization, this could be an adaptive behavioral response to avoid the area.

The interpretations of this study are limited due to our sample size and lack of systematic behavioral data. Nevertheless, considering the difficulties in collecting data prior and after such unexpected stress events, this opportunistic study provides important contributions to primatology. First, it validates an EIA for measuring FGCMs in this species. Second, it demonstrates how the ratio of two adrenal hormones is useful for distinguishing acute versus chronic stress by comparing these hormones in two different stress events. Third, it suggests that stress levels measured by hormones vary by individual, despite their apparent similarities in behavioral changes.

Conclusions

Our results show that the stress response in the months after the death of a group member was not consistent across individuals of this gibbon family, and it seems to be influenced by kin relationships or social dynamics. Although our data are inconclusive due to our small sample size and opportunistic sampling, this study validates an EIA to measure FGCMs in gibbons, and it promotes the inclusion of the FGCMs:DHEAS in subsequent primate behavioral studies to evaluate their stress response.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10329-024-01145-5.

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Data availability The datasets generated and/or analyzed during the current study are available in the Open Access Kent State (OAKS) database https://oaks.kent.edu.

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