

# Examining the dual hormone hypothesis in wild male mountain gorillas (*Gorilla beringei beringei*)

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## ABSTRACT

The Challenge Hypothesis is an influential framework for understanding how androgens are involved in the promotion of competitive behavior during mating-related challenges and has been tested extensively in studies across scientific disciplines. Mixed support in psychological research led scholars to develop the Dual Hormone Hypothesis as a potential path forward, which argues that glucocorticoids moderate the relationship between androgens and status-striving. In the current study, we examine the Challenge Hypothesis and the Dual Hormone Hypothesis in wild male mountain gorillas, representing the first time the latter hypothesis has been tested in a non-human primate. In a sample of 30 adult males comprising over 600 days of observation, we find some limited support for the Challenge Hypothesis. Greater daily rates of targeted aggression toward other adult males corresponded to higher fecal androgen metabolites 1–2 days following observations, though this pattern did not fully generalize to dominance rank or other competitive behaviors examined. However, we find no support for the Dual Hormone Hypothesis: neither dominance rank nor any category of competitive behavior was predicted by the interaction between androgens and glucocorticoids. We close by discussing how this initial investigation might be leveraged toward the development of an expanded Dual Hormone Hypothesis that draws on the large evidence base in primate behavioral ecology.

## 1. Introduction

Testosterone is a gonadal hormone crucial for basic aspects of male reproductive physiology and sexual functioning (Dixon, 1998). Across animal taxa, testosterone is also broadly linked to behaviors that facilitate reproductive opportunities, such as courtship and competition for access to mates. Associations between testosterone and competition, status-seeking, and aggression in males comprise an extensive literature in behavioral endocrinology, with data from numerous contexts and animal taxa (reviewed in e.g. Hirschenhauser and Oliveira, 2006; Archer, 2006). Much of this research is organized under the framework of the Challenge Hypothesis. This hypothesis, originally developed in the context of avian studies but later expanded to other lineages, including primates (Wingfield et al., 1990; Muller, 2017; Grebe et al., 2019b), emphasizes the need for organisms to balance the costs and

benefits of testosterone.

Under its typical formulation, the Challenge Hypothesis predicts that when presented with a mating-related challenge (e.g., the initiation of the breeding season, direct intrasexual competition, a threat to social status, or pursuit of receptive mating partners), testosterone concentrations increase to facilitate an effective competitive response. As high testosterone levels are energetically costly to maintain (Muller and Wrangham, 2004) and may interfere with paternal care behaviors in some species (Rosenbaum and Gettler, 2018), testosterone drops in situations that call for caregiving rather than intrasexual competition. Stemming from this original framing, most work on the Challenge Hypothesis focuses on males, though some scholars have advanced versions that apply to females as well (Rosvall et al., 2020; Grebe et al., 2022).

Empirical support for central predictions of the Challenge Hypothesis is uneven. Consistent with early research linking testosterone and

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territorial aggression in seasonally breeding birds (Wingfield et al., 1990), meta-analyses in humans have generally concluded modest but detectable support for associations between testosterone and status-striving behavior such as aggression (Archer et al., 1998; Archer et al., 2005; Geniole et al., 2020), risk-taking (Kurath and Mata, 2018), and competition outcome (Geniole et al., 2017; but see van der Meij et al., 2016 for a meta-analysis suggesting no relationship between testosterone and leadership.) At the same time, a broad view of the literature that considers diverse human populations (e.g., Muller et al., 2009) and the weight of evidence from other animal taxa (e.g., Hirschenhauser and Oliveira, 2006; Muller, 2017; Goymann et al., 2019; Moore et al., 2020) highlights how these associations may not generalize across species or contexts.

One proposed path to address these limitations focuses on interactions between two neuroendocrine systems—the hypothalamus-pituitary-gonadal (HPG) axis, which produces androgens including testosterone, and the hypothalamus-pituitary-adrenal (HPA) axis. The main end product of the HPA axis in primates, cortisol, is a hormone often released in response to stressors, such as predation, resource scarcity, unstable social relationships, or unpredictable environmental conditions. These cortisol increases, which may help regulate long-term energy maintenance (Romero and Beattie, 2022), have been proposed to interfere with competing organismal responses to reproductive or immune challenges (Morey et al., 2015; Whirledge and Cidlowski, 2013). Conversely, these metabolic effects could instead facilitate activities promoted by testosterone (Ketterson and Nolan Jr, 1999; Shirtcliff et al., 2015). In either scenario, however, cortisol might have a direct impact on many testosterone-associated behaviors. Additionally, the HPA axis and the HPG axis appear to have reciprocal physiological interactions (Viau, 2002; Toufexis et al., 2014). For example, ACTH, an HPA axis hormone that stimulates the release of glucocorticoids, increases in response to estrogen in female rodents and primates but decreases in response to testosterone in males of the same taxonomic groups (Giusani et al., 2000; Viau and Meaney, 1996). Consistent with this, repeated or chronic activation of the HPA axis decreases the presence of sex steroid hormones in rhesus macaques (Norman and Smith, 1992).

The Dual Hormone Hypothesis is a specific framework within human behavioral endocrinology that appeals to these aforementioned hormonal interactions. It proposes that high concentrations of glucocorticoids produced by the HPA axis inhibit the effects of testosterone on dominance and status-striving behaviors (Mehta and Josephs, 2010; Knight et al., 2020). In the original test of the Dual Hormone Hypothesis, researchers conducted two studies to analyze the influence of cortisol on the relationship between testosterone and dominance. In both studies, neither testosterone, cortisol, nor the testosterone/cortisol ratio predicted status-striving behaviors, though the testosterone  $\times$  cortisol interaction did: testosterone predicted dominance in Study 1 only when concurrent cortisol was low, and testosterone predicted men's choices to re-compete in Study 2 after losing a competition only at low concurrent concentrations of cortisol (Mehta and Josephs, 2010).

Following this initial presentation of empirical support, a number of subsequent studies were conducted under a Dual Hormone Hypothesis framework examining interactive effects of testosterone and cortisol on a wide variety of competitive and status-seeking behaviors in humans. These studies revealed a mix of supportive (i.e. attenuating) testosterone  $\times$  cortisol interactions, as well as opposing (i.e. potentiating) interactions, null results, and moderated dual hormone effects (i.e., testosterone  $\times$  cortisol interactions that themselves depend on a third variable; reviewed in Mehta and Prasad, 2015; Grebe et al., 2019a; Dekkers et al., 2019). Ongoing research on the Dual Hormone Hypothesis in humans has emphasized the need for more precise theoretical estimands and the potential importance of environmental contexts in predicting how dual hormone effects relate to behavior (Grebe et al., 2019a; Knight et al., 2020).

Despite clear scholarly interest in further development of the Dual Hormone Hypothesis, one potential path forward has been entirely

unexplored: the use of comparative non-human primate models. Just as comparative research has advanced our understanding of the diversity and commonality in testosterone-behavior interactions, our understanding of Dual Hormone effects may benefit from non-human primate studies. To our knowledge, the Dual Hormone Hypothesis has not been tested in any non-human primate study to date.<sup>2</sup> We provide such a test with an investigation of how androgens (specifically, fecal androgen metabolites or FAMS), glucocorticoids (specifically, fecal glucocorticoid metabolites or FGCMs), and their interaction predict behavioral outcomes and attained status in adult male mountain gorillas (*Gorilla beringei beringei*).

Mountain gorillas are particularly attractive models for studying different frameworks of androgen-behavior interactions due to their clear investment in high levels of putatively androgen-associated morphology and behavior (Rosenbaum et al., 2021). Classic mountain gorilla socioecology consists of one male, several females, and offspring; these groups tend to have strong male-female and male-offspring relationships and weak same-sex relationships (Harcourt, 1979a, 1979b; Rosenbaum et al., 2016). While the modal group contains only one adult male, groups with multiple adult males occur regularly in this gorilla subspecies (Caillaud et al., 2014; Robbins and Robbins, 2018). Multi-male groups typically form from males becoming silverbacks in their natal groups, from all-male groups who manage to attract transferring females, or from splits of existing multimale groups (Stoinski et al., 2009a; Vigilant et al., 2015). It is extremely rare for an adult male to transfer into a heterosexual group (Harcourt, 1978; Stoinski et al., 2009b). Intrasexual competition is particularly salient for male mountain gorillas, who compete with other adult males, particularly those from other groups, for access to mates and to protect their offspring from infanticide (Robbins et al., 2013; Mirville et al., 2018).

Two sets of predictions motivate the present study of male mountain gorillas. First, as the Challenge Hypothesis posits that androgens respond to reproductive competition, this hypothesis predicts positive associations between androgens and the manifestations of status-striving and aggression regularly collected in observational data on wild mountain gorillas: 1) diffuse acts of competitive behavior, such as vocalizations and displays; and 2) targeted acts of competitive behavior such as coming to physical blows. We also assess whether a measure of attained status, dominance rank, correlates with androgens. While the original formulation of the Challenge Hypothesis does not necessarily predict that androgens should increase with rank, many have argued that the hypothesis suggests such a link in non-human primates where rank is mediated via competitive behavior (see e.g., Muller and Wrangham, 2004; Marshall and Hohmann, 2005; reviewed in Rosenbaum et al., 2020). Two recent studies found no significant relationship between androgens and rank in mountain gorillas (Rosenbaum et al., 2020; Rosenbaum et al., 2021). This null effect could be due to the use of a single variable (dominance rank) that does not adequately capture status-striving—we investigate this possibility here. Alternatively, null results might arise due to effects of androgens that are conditional on glucocorticoids. We address this possibility and expand the scope of hormone-behavior investigation in mountain gorillas by examining a second set of predictions that stems from the Dual Hormone Hypothesis: androgens and glucocorticoids should interact to predict rank and competitive behaviors (diffuse and targeted), such that associations between androgens and these variables are conditional upon concurrent concentrations of glucocorticoids. Interestingly, a recent review of the Dual Hormone Hypothesis (Knight et al., 2020) suggests that attained status might be more likely to capture Dual Hormone interactions than behavioral manifestations of status-striving—we also examine this

<sup>2</sup> While Greenberg et al. (2022) discuss the Dual Hormone Hypothesis in their study of androgens, glucocorticoids, and male status in vervet monkeys, they do not report the results of the canonical androgen  $\times$  glucocorticoid interaction on any outcome variables.

possibility.

## 2. Methods

The mountain gorillas in this study (30 adult males >10 years of age) lived in 10 mixed-sex social groups monitored by the Dian Fossey Gorilla Fund in Volcanoes National Park, Rwanda. Four of these groups were single-male, and six were multimale. Adult male number in these groups ranged from two to twelve, with the exact number fluctuating across the study period (Table 1).

Rainfall is bimodally distributed, with a long and short wet season lasting from September to December and March to May, respectively (Eckardt et al., 2019). Our overall dataset stems from the time period of April 2011–December 2012, when both fecal samples and focal behavioral data were collected intensively.

### 2.1. Fecal sample collection

We aggregated samples originally collected for a range of projects focused on fecal androgen metabolites (FAMs), fecal glucocorticoid metabolites (FGCMs), and behavior (see e.g. Eckardt et al., 2016; Rosenbaum et al., 2021). We measure these metabolites because native cortisol and testosterone are not typically excreted in primate fecal samples in significant quantities, and metabolites serve as validated proxies for cortisol and testosterone (Eckardt et al., 2016; Rosenbaum et al., 2021; Grebe et al., 2023). Between 0700 h and 1600 h on a given observation day (for a maximum 4 h duration), trained observers collected fecal samples uncontaminated with rainwater, urine, or other gorillas' fecal material. Samples were placed in a cooler bag with an ice pack after collection and placed in a –20 °C freezer upon returning from a field day. All hormone extractions were completed within 2–3 months of sample collection using a validated, field-friendly technique (Eckardt et al., 2016; Santymire and Armstrong, 2010). After extraction, samples were dried down, capped, and returned to the –20 °C freezer until shipment to laboratories in the US. All evaporated extracts were kept frozen at –20 °C until being reconstituted for use in hormonal assays.

Our rank analyses focus on 1104 samples collected from males in multimale groups whose ranks were known ( $n = 24$ ), and our behavioral analyses focus on 639 samples from 27 males collected 24–48 h after focal behavioral observations (described below). While gut passage time for FAMs has not been directly tested, they peaked in this time window after four competitive events examined in Rosenbaum et al. (2021). Any samples collected in this 24–48 h window following focal observations were paired to create one observation; we averaged hormone metabolite values when multiple samples were collected in this window. Prior research suggests that increases in FGCMs following a major stressful event may follow a slower time course, with a peak at approximately three days (Eckardt et al., 2016). In supplementary analyses (Table S1, Figs. S1 and S2), we repeat the analyses presented in our results using a 3-day window.

**Table 1**

Group composition during the study period.

| Group | Adult male modal number (range) | Adult female modal number (range) |
|-------|---------------------------------|-----------------------------------|
| BWE   | 1 (1)                           | 3 (3–5)                           |
| GIR   | 1 (1)                           | 1 (1)                             |
| INS   | 1 (1)                           | 1 (1–3)                           |
| ISA   | 2 (1–2)                         | 6 (4–6)                           |
| KUY   | 2 (2–3)                         | 4 (3–5)                           |
| NTA   | 3 (3)                           | 3 (3–4)                           |
| PAB   | 9 (8–12)                        | 11 (11)                           |
| TTT   | 4 (3–4)                         | 1 (1)                             |
| UGE   | 2 (2)                           | 3 (3–4)                           |
| URU   | 1 (1)                           | 2 (2)                             |

### 2.2. Behavioral data collection

Behavioral data primarily stem from 50-min focal follows of adult males by experienced field staff. The target number of daily focal follows per individual during the study period was four (i.e., 3.33 h of observation time), though actual time observed varied slightly (mean: 3.17 h; SD: 0.40 h). We determined dominance rank in males as described in Stoinski et al. (2009b) and Rosenbaum et al. (2021). Briefly, we assigned an ordinal dominance rank to males in each multimale group based on the observed pattern of non-aggressive displacement and avoidance behaviors (i.e., events where the approach of one animal within 5 m caused the retreat of another), which were recorded continuously over the study period. As there was sometimes an insufficient number of displacements to determine specific ranks of some lower-ranking males, we distinguish between the top three positions (*alpha*, *beta*, *gamma*) and place all males ranked fourth or lower into a single category called *subordinate*. In two cases where ranks involving males outside the subordinate category were ambiguous due to insufficient interactions (one involving gamma versus subordinate, the other involving alpha versus beta), we relied on the judgment of experienced observers familiar with the groups, including authors SR and WE. In both cases, they concurred that the older animal was dominant over the younger one for the period covered by our study. The only rank change during the study period occurred when a gamma-ranked male moved to beta rank after the beta male in his group disappeared.

Regarding status-striving/competitive behavior, our analyses focus on daily incidences of fifteen relevant behaviors (for ethogram, see Table 2). Some of these behaviors were relatively common (e.g., displays), whereas others occurred only rarely during the study (e.g., contact aggression, such as biting or kicking). Thus, we calculated three composite categories to use in our primary analyses: 1) the daily total of *diffuse competitive behaviors*, which includes all incidences of vocal aggression and displays; 2) the daily total of *targeted competitive behaviors*, which includes all incidences of non-contact or contact aggression; and 3) the daily sum total of *all competitive behaviors* listed in Table 2. Each of these composites was further categorized by the age-sex category of the recipient (adult males over 10 years old, males under 10 years old, or female). To maximize the available sample size for our

**Table 2**

Ethogram of target competitive behaviors.

| Category               | Example behaviors <sup>a</sup>                                                                                                                                   |
|------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Display                | Diffuse competitive behavior                                                                                                                                     |
|                        | <b>Chest beat:</b> slapping chest alternatively with hands                                                                                                       |
|                        | <b>Ground slap:</b> thumping ground with hands                                                                                                                   |
|                        | <b>Object display:</b> shaking/throwing/thrashing object in environment                                                                                          |
|                        | <b>Symbolic feeding:</b> placing vegetation between lips                                                                                                         |
| Vocal aggression       | <b>Run:</b> animal runs for a short distance, often while hooting or object displaying                                                                           |
|                        | <b>Hooting:</b> vocalization usually preceding other display types                                                                                               |
|                        | <b>Pig grunt:</b> aggressive vocalization that sounds like coughing (if in response to pig-grunts or screams from animals out of view, recorded as no recipient) |
|                        | <b>Scream:</b> high-pitched aggressive vocalization                                                                                                              |
| Contact aggression     | Targeted competitive behavior                                                                                                                                    |
|                        | <b>Kick:</b> animal kicks another                                                                                                                                |
|                        | <b>Hit:</b> animal slaps, hits or strikes another                                                                                                                |
|                        | <b>Bite:</b> animal bites or slashes another with canines                                                                                                        |
|                        | <b>Grab:</b> contact through grabbing another individual                                                                                                         |
|                        | <b>Drag:</b> dragging another individual                                                                                                                         |
| Non-contact aggression | <b>Lunge:</b> animal rushing at another in short, fast run, without striking (if animal hits another animal at the end, recorded as two separate events)         |
|                        | <b>Chase:</b> one animal actively pursues another at a run, with clear aggressive intent                                                                         |

<sup>a</sup> Many of the behaviors described also occur during play. Observers are trained to distinguish between playful and aggressive intent during interactions.

analyses, data collected during focal follows was supplemented with selected data collected ad libitum—specifically, incidences of contact aggression were recorded from non-focal animals whenever they were opportunistically witnessed within a group. These incidences were adjusted for group observation time (see *Data Analysis*). In total, our analysis contains 2149 h of focal observations.

### 2.3. Hormonal assays

FAMs and FGCMs were measured with enzyme-linked immunoassays (EIAs) that have been previously validated for use with mountain gorilla fecal samples, as described in Eckardt et al. (2016), Rosenbaum et al. (2021), and Grebe et al. (2023). All FGCM values were generated at the Lincoln Park Zoo's Davee Center for Epidemiology and Endocrinology laboratory using in-house assays (antibody R4866, CJ Munro, UC-Davis). Due to this lab closing, some FAM values were obtained using the Lincoln Park Zoo's in-house assay (antibody R156/7, CJ Munro, UC-Davis), while others were obtained at the University of Michigan's Primate Behavior Lab using a commercial kit designed for wildlife researchers (Arbor Assays ISWE Testosterone Mini-Kit; Catalog #ISWE-001). We standardized FAM results within assays before combining for analysis (see *Data Analysis* section below). In all cases, only results from samples with an intra-assay coefficient of variation (CV) <15 % were used for analysis. Inter-assay CV for FGCM assays performed at the Lincoln Park Zoo was 12.7 %; for FAM assays performed at the Lincoln Park Zoo, 9.4 %; for FAM assays completed at the University of Michigan, 9.2 %. In our overall dataset of FAM and FGCM values ( $n = 1807$ ; this number includes measurements without accompanying behavioral observations), the two hormone metabolites were moderately positively correlated ( $r = 0.25$ ,  $p < 0.001$ ).

### 2.4. Data analysis

Our modeling strategy differed between the two broad classes of status-relevant variables we analyzed. While rank, as a direct measure of attained status, has been argued to be a particularly relevant target for examining dual hormone associations (cf. Knight et al., 2020), the almost complete lack of within-individual variation in rank in our study (only one male changed ranks during the study period) precludes its use as an outcome variable for analyses. We instead examined ordinal rank in multimale groups by using it as a predictor of a) FAM concentrations (i.e., testing a Challenge Hypothesis-inspired prediction; this analysis replicates and builds upon the results presented in Rosenbaum et al., 2021 with additional samples assayed since that paper's publication); and b), the standardized difference between FAMs and FGCMs in a given sample (i.e. z-scored FAMs – z-scored FGCMs; this represents a Dual Hormone Hypothesis-inspired prediction examining FAMs relative to FGCMs across ranks). These linear mixed-effects models (*lme4* package in R; Bates et al., 2015) included random intercepts for each male to account for uneven repeated sampling of individuals. As covariates, we included the male's age at time of sampling and the number of silverback males in his group.

In contrast, rates of competitive behavior fluctuated throughout the study, enabling us to test the Challenge Hypothesis and the Dual Hormone Hypothesis in a more familiar format: by assessing the main effect of FAMs (i.e., the Challenge Hypothesis), and their interaction with FGCMs (i.e., the Dual Hormone Hypothesis), on rates of these behaviors. Specifically, we used negative binomial generalized linear models (*glmmTMB* package in R; Brooks et al., 2017) to assess hormonal associations with our three behavioral count composites (*diffuse aggression*, *targeted aggression*, and *all competitive behavior*). These models included as covariates the focal male's age at time of observation (a variable that is highly collinear with rank; Rosenbaum et al., 2021), a binary variable indicating whether the focal male was in a single-male or multimale group configuration at the time of observation, and random intercepts for each individual male. For each behavioral outcome, we separately

considered a model predicting that category of behavior directed only toward other adult males (as arguably the most direct proxy of intra-sexual competition) and a model predicting the same category of behaviors directed toward any other gorilla (females and subadult males included). Models of behavioral counts all included an offset term (log-transformed hours observed on a given day) to account for varying exposure time.

Because daily counts of behaviors were heavily zero-inflated, we adopted two strategies to create models that balanced the accurate modeling of outcomes with the ability to examine behaviors that were relatively rare (e.g., targeted contact aggression). First, as described above, we created sum composites of behaviors for diffuse and targeted competitive behavior, in addition to a third composite combining both categories. Second, in each model, we initially included the same set of predictors for a conditional component (i.e. estimating  $\beta$ , the proportional effect of predictors on the outcome behavior, given that the outcome was greater than zero) and a zero-inflation component (estimating  $\beta^{zi}$ , the proportional effect of predictors on the odds of whether an outcome was zero versus greater than zero). Models that include both of these parameters simultaneously are commonly known as hurdle models (Heiss, 2022). In some cases, which we identify in our results below, we encountered convergence issues with zero-inflation components and removed them from our model specifications. To visualize these models, we present expected value plots in our results that show model-based estimations jointly considering the effects of conditional and zero-inflation parameters on outcome variables. See Brooks et al. (2017) and Heiss (2022) for applied introductions to specifying, interpreting, and plotting predicted values from hurdle models.

In all models, whether assessing rank or competitive behavior, hormone metabolite concentrations were log-transformed and z-scored within assay type (1 type for FGCMs, 2 types for FAMs) prior to analysis, to standardize predictors and account for known differences in means and standard deviations between assays. For each model, we verified model fit by inspecting the deviation, dispersion, and outliers of residuals using the *DHARMa* package (Hartig, 2022). To interpret the results from statistical models, we estimated pairwise differences and plotted marginal trends using the *emmeans* package (Lenth, 2023) and the *marginalEffects* package (Arel-Bundock, 2023). All R code and behavioral data have been posted publicly on the Open Science Framework at <https://osf.io/4t3cz/>; access to hormonal data is restricted by the Rwanda Development Board and can be requested via contacting author NMG.

## 3. Results

### 3.1. Challenge hypothesis: fecal androgen metabolites

#### 3.1.1. Rank

Replicating and extending the results reported in Rosenbaum et al. (2021) with a larger sample ( $n = 1104$ ), higher male rank did not predict higher FAMs. To the contrary, while FAMs did overall vary across ranks ( $\chi^2(3) = 15.92$ ,  $p = 0.001$ ), gamma males had the highest age-adjusted, standardized FAMs ( $\bar{x} = 0.50$ ,  $SE = 0.17$ ), significantly higher than alpha ( $\bar{x} = -0.57$ ,  $SE = 0.16$ ; pairwise  $p < 0.001$ ) and beta ( $\bar{x} = -0.08$ ,  $SE = 0.10$ ;  $p = 0.006$ ) males. Subordinate male age-adjusted FAMs ( $\bar{x} = 0.47$ ,  $SE = 0.24$ ) were also significantly higher than alpha males (pairwise  $p = 0.007$ ). No other pairwise comparisons between ranks reached statistical significance ( $p > 0.05$ ).

#### 3.1.2. Status-striving behavior

FAM concentration did not significantly predict overall rates of competitive behavior toward other adult males in the conditional component of our model ( $\beta = -0.14$ ,  $p = 0.430$ ), though this parameter was significantly negative in the zero-inflation component ( $\beta^{zi} = -2.76$ ,  $p = 0.023$ ). In other words, lower FAM concentrations predicted a higher likelihood of not engaging in competitive behavior at all, but conditional



on a non-zero level of this behavior, FAMs did not predict rates of it. These patterns together produce the expected values derived from the model in Fig. 1: relatively low competitive behavior at low concentrations of FAMs, a peak at intermediate FAMs, and intermediate amounts of competitive behavior at high FAMs.

These results did not hold when expanding the outcome to encompass competitive behaviors directed toward any target (females and subadult males included). In this model, FAMs were not a significant predictor in either component ( $\beta = -0.09$ ,  $p = 0.090$  and  $\beta^{zi} = -0.20$ ;  $p = 0.953$ ).

Next, we considered targeted competitive behavior only, first toward other adult males. Though there was not sufficient variation in this outcome to separately estimate a zero-inflation component of this model, we found a positive effect of FAMs in our conditional model ( $\beta = 0.57$ ,  $p = 0.001$ ). Greater FAM concentrations predicted higher rates of targeted competitive behavior toward other males (Fig. 2). FAMs were no longer a significant predictor of targeted competitive behavior when broadening targets to include females and subadult males ( $\beta = 0.06$ ,  $p = 0.412$ ).

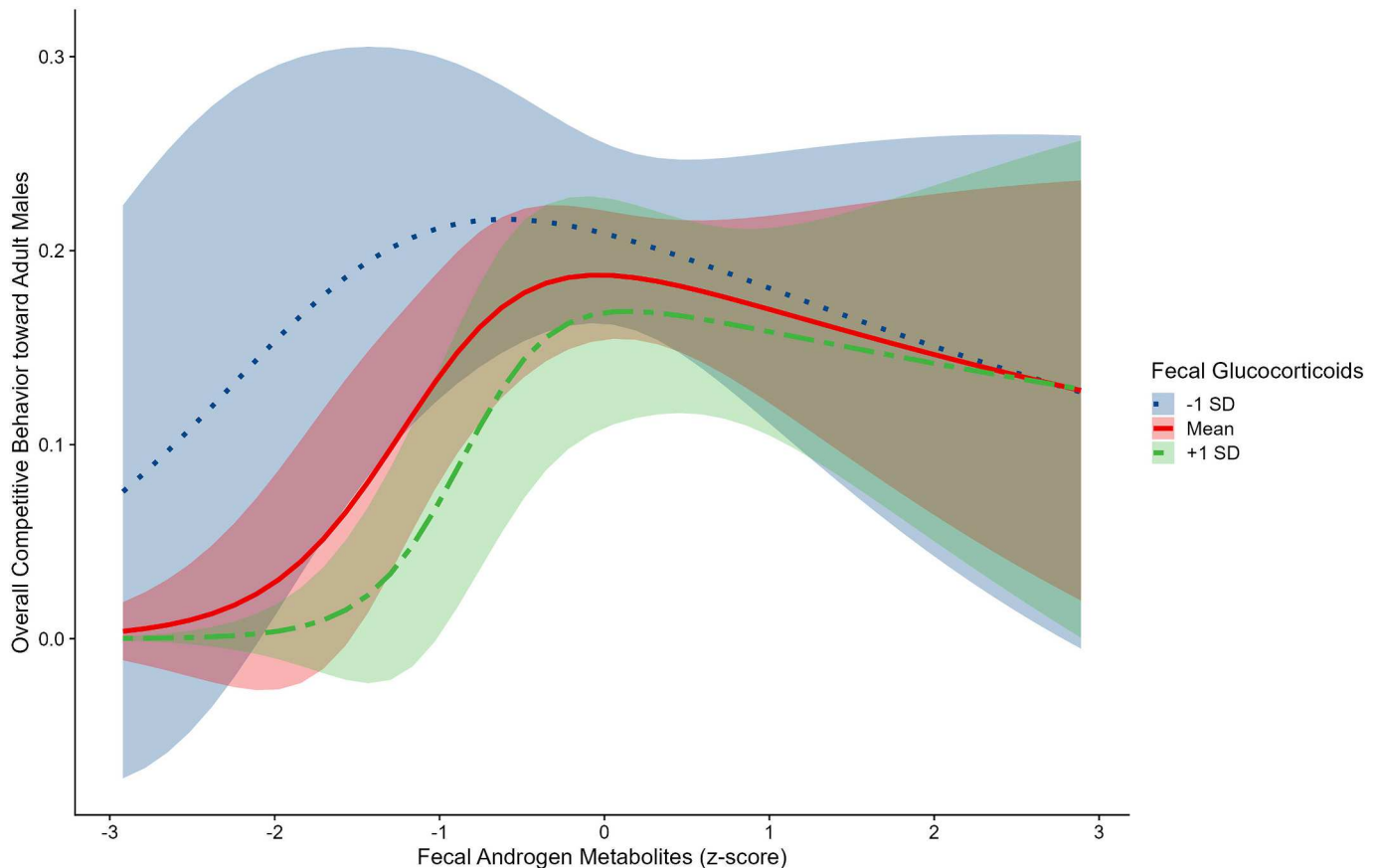
Finally, moving to diffuse competitive behavior toward other adult males, we found a significant negative conditional effect of FAMs ( $\beta = -0.74$ ,  $p = 0.007$ ) in addition to a negative zero-inflation effect ( $\beta^{zi} = -2.71$ ,  $p = 0.045$ ); together, these parameters produce a distribution similar to that for overall competitive behavior, such that rates of diffuse competitive behavior were greatest at intermediate FAM concentrations (Fig. 3).

### 3.2. Dual hormone hypothesis: fecal androgen metabolite $\times$ fecal glucocorticoid metabolite interaction

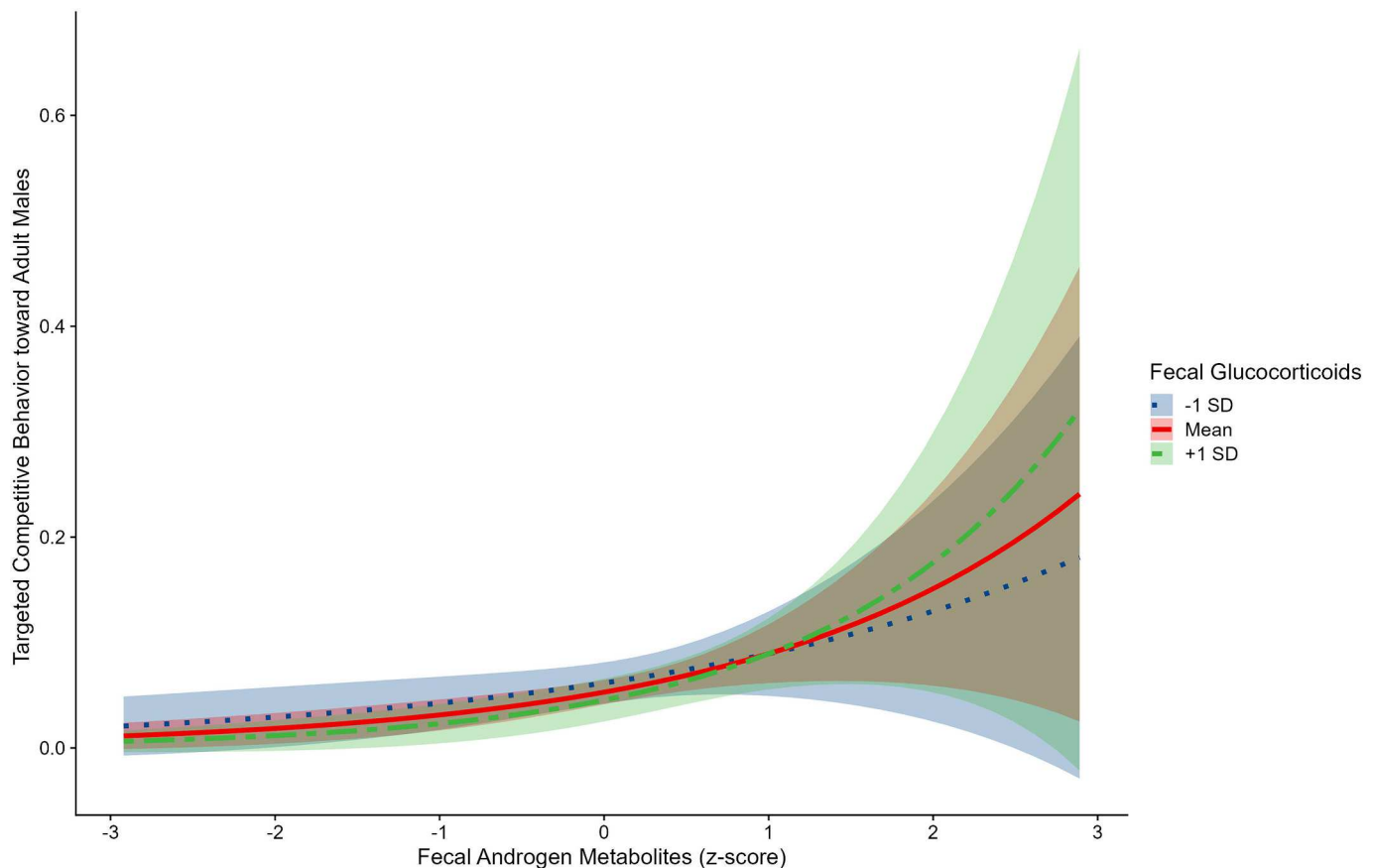
#### 3.2.1. Rank

Higher ranking males did not have systematically higher FAMs relative to FGCMs than males of other ranks (Fig. 4). While the omnibus comparison between ranks was once again significant overall ( $\chi^2(3) = 8.96$ ,  $p = 0.030$ ), gamma males on average had the highest age-adjusted, standardized FAM - FGCM difference ( $\bar{x} = 0.76$ ,  $SE = 0.21$ ). This was significantly higher than alpha males ( $\bar{x} = -0.16$ ,  $SE = 0.20$ ; pairwise  $p = 0.012$ ) or beta males ( $\bar{x} = 0.18$ ,  $SE = 0.14$ ; pairwise  $p = 0.020$ ), but not significantly higher than subordinates ( $\bar{x} = 0.46$ ,  $SE = 0.29$ ; pairwise  $p = 0.297$ ). No other pairwise differences between ranks were statistically significant (all  $p > 0.05$ ).

Additionally, as the overlapping confidence intervals in Figs. 1–3 suggest, the FAM  $\times$  FGCM interaction was not a significant predictor of any of our behavioral outcomes. This was the case for overall competitive behavior toward adult males in both the conditional ( $\beta = 0.05$ ,  $p = 0.719$ ) and zero-inflation components ( $\beta^{zi} = -1.18$ ,  $p = 0.103$ ). These null parameter estimates did not qualitatively shift when expanding the outcome to encompass competitive behavior toward any target, ( $\beta = -0.07$ ,  $p = 0.222$ ;  $\beta^{zi} = 1.84$ ;  $p = 0.559$ ). The FAM  $\times$  FGCM interaction predicting targeted aggression, whether directed toward adult males ( $\beta = 0.17$ ,  $p = 0.280$ ) or any target ( $\beta = -0.08$ ,  $p = 0.283$ ), were similarly non-significant. Finally, the FAM  $\times$  FGCM interaction failed to significantly predict diffuse aggression, either toward adult males ( $\beta = -0.17$ ,  $p = 0.409$ ) or toward any target ( $\beta = -0.07$ ,  $p = 0.393$ ).



**Fig. 1.** Frequency of males' overall competitive behavior toward other adult males as predicted by fecal androgen (FAM) and fecal glucocorticoid metabolite (FGCM) concentrations, after controlling for age, group composition (single versus multi-male group), and specifying random intercepts for individual animals. These model-derived expected values are obtained from the combined conditional and zero-inflation components of our statistical model.



**Fig. 2.** Frequency of males' targeted competitive behavior toward other adult males as predicted by fecal androgen (FAM) and fecal glucocorticoid metabolite (FGCM) concentrations, after controlling for age, group composition (single versus multi-male group), and specifying random intercepts for individual animals. These model-derived expected values are obtained from the conditional component of our statistical model only.

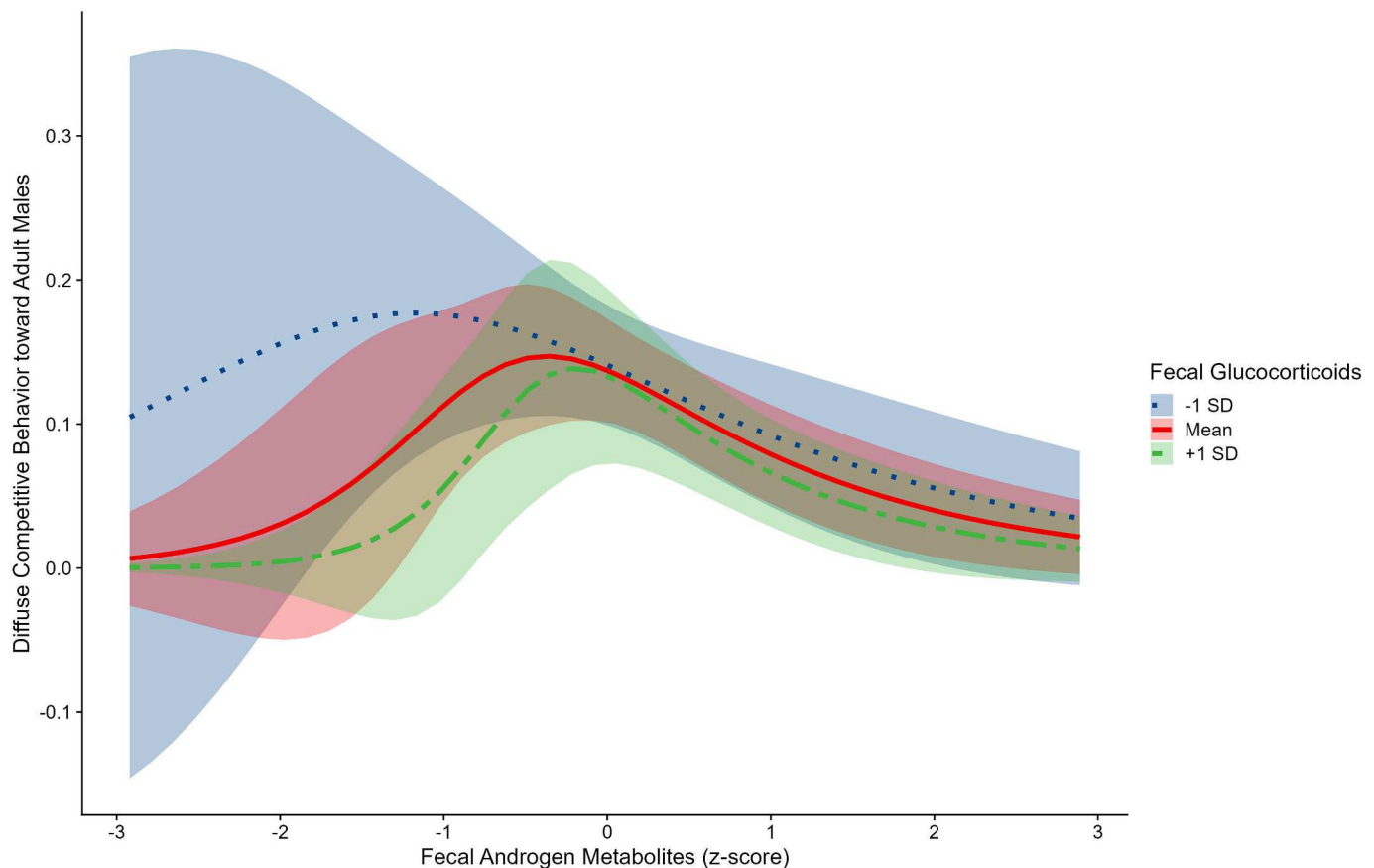
#### 4. Discussion

The morphology and behavioral patterns of adult male mountain gorillas suggest a strong, persistent reliance on intrasexual competition, positioning them as attractive models for investigating the relationships between competitive behavior, status, and androgens (i.e., the Challenge Hypothesis). Despite this clear rationale, a recent analysis of rank and androgens in this species yielded null results (Rosenbaum et al., 2021). In the present study, we sought to expand upon this initial investigation in two ways. First, we moved beyond rank and additionally considered a variety of competitive behaviors as potential indicators of status-striving. Second, we turned to a framework within the field of human social endocrinology that was generated, at least in part, to explain null relationships between androgens and status-striving: the Dual Hormone Hypothesis (Mehta and Josephs, 2010; Knight et al., 2020). This framework, which appeals to the moderating influence of glucocorticoids, has been examined extensively in humans, but despite its underlying arguments applying across species it had yet to be tested in any non-human primate.

Overall, we find uneven support for the Challenge Hypothesis, and no support for the Dual Hormone Hypothesis. As previously reported, rank and androgens appear to be unrelated (Rosenbaum et al., 2020; Rosenbaum et al., 2021). One category of behavior—targeted aggression toward other adult males—showed the predicted positive relationship with androgens. Diffuse aggression, and the sum of all competitive behavior, exhibited a more complex pattern: while higher androgens appeared to lower the likelihood of a male exhibiting no competitive behavior, overall these behaviors were most frequent at intermediate androgen concentrations. One potential interpretation follows the

conclusions of van der Meij et al. (2016) in their analyses of testosterone and human leadership. They argue that relatively low-status individuals with strong status-striving motivation have relatively high testosterone concentrations, even if this behavior does not lead to actual status attainment—this may explain why androgens in our study were linked to some competitive behaviors, but not to rank. Regardless of how one interprets our main effects of androgens, however, glucocorticoids did not modify any of these associations—in other words, we do not see a ‘canonical’ Dual Hormone effect in male gorillas akin to those reported in the human literature. In a recent review of the Dual Hormone Hypothesis, Knight et al. (2020) suggested that direct measures of status might be more likely to capture Dual Hormone interactions than behavioral manifestations. Our data, which have the advantage of including both, also do not support this argument, as Dual Hormone effects did not follow the expected patterns across outcomes. Below, we reflect on the implications of our results for the Dual Hormone hypothesis, and for social endocrinology studies in wildlife more generally.

One challenge in adapting the Dual Hormone Hypothesis to a study of wild non-human primates concerns necessary differences in how the hypothesis is tested. Most prominently, our observational study relied on opportunistic fecal sampling for hormone measurement, which raises at least two issues for interpretation. First, fecal samples that represent a composite of hormonal secretion over many hours do not have the same temporal resolution as Dual Hormone studies in humans that rely on other media, such as blood or saliva. To capture endocrine changes that corresponded to behavior, we targeted a gap between time of fecal sampling and behavioral events based on existing evidence from studies of mountain gorillas that show reliable increases in fecal hormone metabolites following relevant socioecological events (Eckardt et al., 2016;



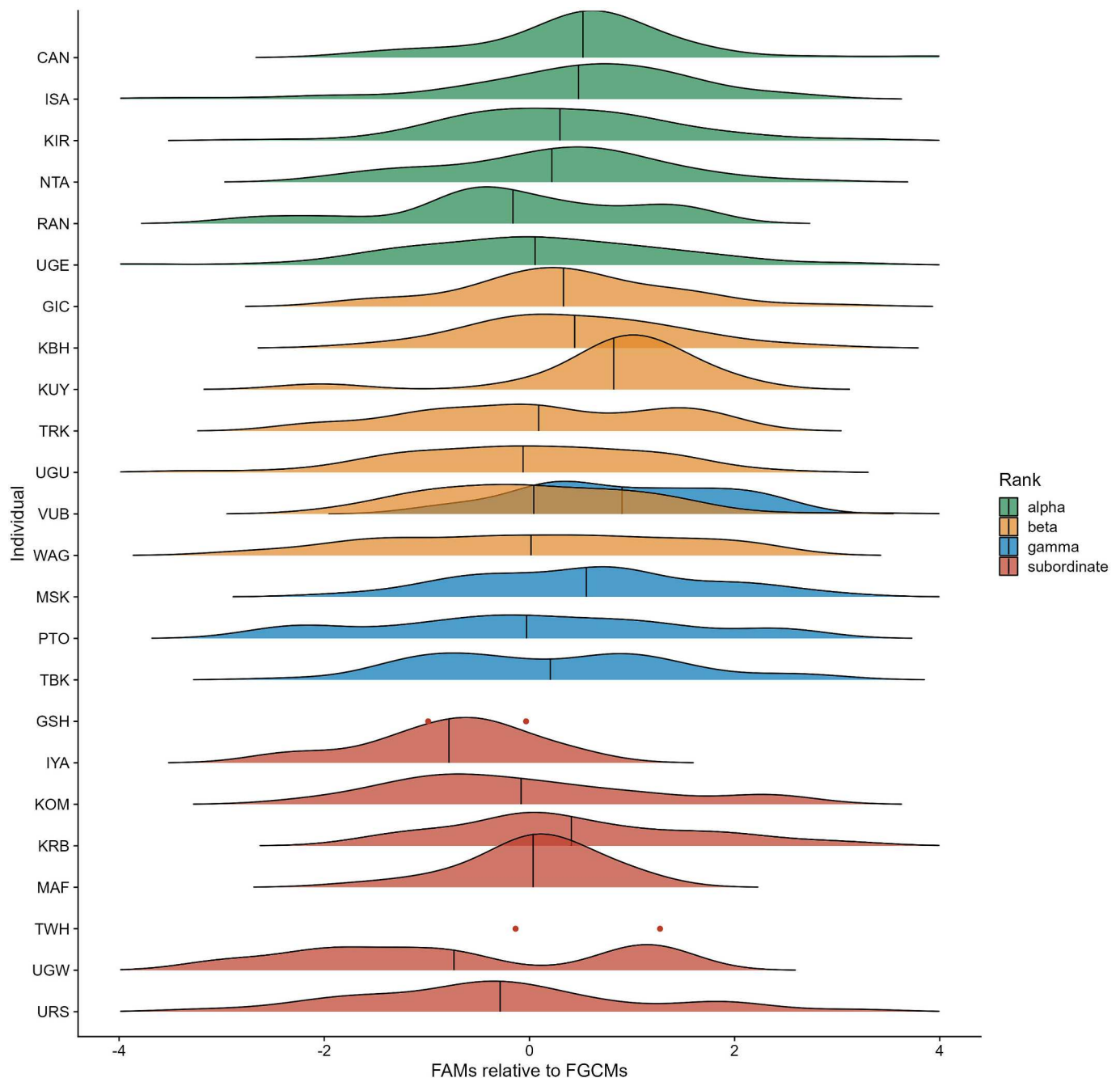
**Fig. 3.** Frequency of males' diffuse competitive behavior as predicted by fecal androgen (FAM) and fecal glucocorticoid metabolite (FGCM) concentrations, after controlling for age, group composition (single versus multi-male group), and specifying random intercepts for individual animals. These model-derived expected values are obtained from the combined conditional and zero-inflation components of our statistical model.

Rosenbaum et al., 2021). At the same time, we acknowledge the possibility that measurement of fecal hormone metabolites, representing a relatively 'diffuse' and perhaps noisy approach relative to measurement of other sample types, along with our observation periods that only cover up to four hours per day, may have made it more difficult to detect Dual Hormone effects. Second, many Dual Hormone studies in humans rely on hormone concentrations, or changes in concentrations, relating to tasks or experimental manipulations chosen by researchers: for example, earnings, risk-taking, or punishment decisions in economic games (e.g. Pfattheicher et al., 2014; Akinola et al., 2016; Mehta et al., 2017; Ronay et al., 2018). In contrast, we focused on examining associations between hormone metabolites and corresponding natural variations in behavior. Large changes in hormonal secretion may be restricted to rarer occurrences in the lives of mountain gorillas—for instance, protracted intragroup fights over mating opportunities, or intergroup male competition (see Eckardt et al., 2016; Rosenbaum et al., 2021). Most of our data record less intense bouts of competitive behavior, which conceivably correspond to smaller hormone changes that are more difficult to reliably detect.

Notably, however, the above interpretational issues equally apply to tests of the Challenge Hypothesis. And despite potential limitations, there are also strengths to our observational design. Our focus on naturally occurring behaviors provides a degree of ecological validity that experiments may lack. We did observe positive associations between certain competitive behaviors and androgens, suggesting that an approach examining a variety of circumstances that accompany hormonal changes is a viable strategy (indeed, it is the dominant means of examining aggression and androgens in non-human primates: e.g. Lynch et al., 2002; Beehner et al., 2006; Ostner et al., 2011; Negrey et al.,

2023). Our design also allowed us to include a larger sample size than would be possible with a narrower focus on certain behaviors, or with manipulations that only examine scenarios constructed by an experimenter. In sum, we believe our study represents an important but initial venture into the study of hormonal interactions and social behavior in wildlife.

While the Challenge Hypothesis was originally generated from studying wildlife and thus has an extensive body of comparative literature devoted to it, the same is not true of the Dual Hormone Hypothesis. This highlights a key area for theory development and modification. Since comparative research on this hypothesis is in its infancy, there is the opportunity to draw from the rich literature on animal behavioral endocrinology and generate frameworks that accommodate species-specific socioecology in predicting when Dual Hormone effects might emerge. Our study provides an initial example of some considerations for building such a framework. Some scholars have argued that, in humans, present status attainment is an especially promising target for Dual Hormone effects, as its connection to status-striving is clearer than behavioral proxies (Knight et al., 2020). Our experience studying mountain gorillas suggests a different perspective. In this species, status-striving and current status do not necessarily closely follow one another and may even be inversely associated. Males who are not yet high-ranking, but may later rise to that level, appear to engage most frequently in the kinds of competitive behaviors we measured in our study. In contrast, current alpha males expend less effort engaging in displays and aggressive behavior. Indeed, when we simply examine competitive behavior toward other adult males in our dataset, regardless of hormone concentrations, we see the lowest rates in alpha males compared to all other ranks. If the target construct is "status-striving in



**Fig. 4.** Ridgeline plots for individual males in our study, depicting the distribution of observed standardized fecal androgen metabolite (FAM) values minus standardized fecal glucocorticoid metabolite (FGCM) values for each sample. Depicted values are not age-adjusted. Higher values on the x-axis represent greater FAMs relative to FGCMs. Individual means are denoted with a vertical line. Two males were represented by only two samples and are plotted with dots only. Only one male (VUB) occupied two different dominance ranks during the study period.

mountain gorillas”, then perhaps rates of competitive behavior are a more desirable estimand than dominance rank. At the same time, the nature of mountain gorilla society, with its often remarkably stable dominance hierarchies (Robbins et al., 2019), may not generalize to many other wild primates. For instance, chimpanzee dominance hierarchies involve substantial amounts of intragroup aggression and shift comparatively quickly (Bray et al., 2016; Watts, 2018), making rank a potentially more promising target. Consistent with this idea, Negrey et al. (2023) find strong positive correlations between rank and androgens in chimpanzees. In sum, we argue that certain behavioral proxies are not inherently ‘better’ or ‘worse’ targets than attained status, and that the most appropriate choice may vary with the species in question.

Supporting such a focus on species-tailored frameworks, Goymann et al. (2019) suggest a “Challenge Hypothesis 2.0” framework, part of which entails differential predictors of androgen responsiveness depending on species’ mating systems and the timing/extent of paternal care.

Another recent proposal regarding the Dual Hormone Hypothesis concerns the possibility of three-way interactions, in which androgen  $\times$  glucocorticoid interactions are themselves moderated by other social contextual variables in predicting status-striving (e.g., Tackett et al., 2014; Lozza et al., 2017; Knight et al., 2022). For example, distinguishing between competitive behavior that is status-seeking versus status-loss avoiding has been proposed to be a key moderating variable for Dual Hormone effects (Knight et al., 2022). In theory, competitive



behavior directed toward lower-ranking male gorillas would be more consistent with status-loss avoidance, while behavior directed toward higher-ranking males would be more consistent with status-seeking. While this idea is intriguing, our current dataset precludes a robust empirical test of this distinction. A low frequency of intragroup male-male aggression coupled with appropriately timed fecal samples in our data provides few observations where the outcome rate is non-zero. This zero-inflation is also an obstacle for our other behavioral outcomes, but we are able to leverage the information provided by the absence of any kind of competitive behavior as relevant to an individual's overall level of status-striving. In contrast, one cannot further distinguish whether this absence is more consistent with a lack of status-seeking or a lack of status-loss avoidance. In spite of this limitation, we see promise in examining candidate social context variables in wildlife-friendly paradigms and exploring how they might interact with individuals' social endocrinology.

## 5. Conclusion

The field of behavioral endocrinology has been historically and continually characterized by a broad comparative approach, even as the temptation to restrict examination to a few 'model species' has repeatedly proven to be an obstacle (Beach, 1950; Thompson, 2020). We encourage future development of the Dual Hormone Hypothesis to continue in this tradition. Examinations of new moderators and new techniques in human studies of androgens, glucocorticoids, and behavior are welcome initiatives to pinpoint how these hormones might interact within our own species. At the same time, discovering fundamental neuroendocrine mechanisms of behavior requires examining how hormones work across a range of species. As our study exemplifies, these investigations may reveal mechanistic similarities that suggest a common means of achieving fitness goals across taxa, but they might also highlight differences that require accommodation and revised theoretical frameworks.

## CRedit authorship contribution statement

**Nicholas M. Grebe:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation. **Josephine Schmidt:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Winnie Eckardt:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis. **Rose Umuhoza:** Formal analysis, Data curation. **Dominic Mayo:** Writing – review & editing, Writing – original draft, Formal analysis. **Tara S. Stoinski:** Supervision, Project administration, Funding acquisition, Data curation. **Rachel M. Santymire:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Formal analysis, Data curation. **Stacy Rosenbaum:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Data availability

Data and code are publicly available on OSF at <https://osf.io/4t3cz/>.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2024.105588>.

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