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Aggression, glucocorticoids, and the chronic costs of status competition for wild male chimpanzees

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ABSTRACT

Across vertebrates, high social status affords preferential access to resources, and is expected to correlate positively with health and longevity. Increasing evidence, however, suggests that although dominant females generally enjoy reduced exposure to physiological and psychosocial stressors, dominant males do not. Here we test the hypothesis that costly mating competition by high-ranking males results in chronic, potentially harmful elevations in glucocorticoid production. We examined urinary glucocorticoids (n = 8029 samples) in a 20-year longitudinal study of wild male chimpanzees (n = 20 adults) in the Kanyawara community of Kibale National Park, Uganda. We tested whether glucocorticoid production was associated with dominance rank in the long term, and with mating competition and dominance instability in the short term. Using mixed models, we found that both male aggression and glucocorticoid excretion increased when the dominance hierarchy was unstable, and when parous females were sexually available. Glucocorticoid excretion was positively associated with male rank in stable and unstable hierarchies, and in mating and non-mating contexts. Glucorticoids increased with both giving and receiving aggression, but giving aggression was the primary mechanism linking elevated glucocorticoids with high rank. Glucocorticoids also increased with age. Together these results show that investment in male-male competition increases cumulative exposure to glucocorticoids, suggesting a long-term tradeoff with health that may constrain the ability to maintain high status across the life course. Our data suggest that the relationship between social rank and glucocorticoid production often differs in males and females owing to sex differences in the operation of sexual selection.

1. Background

In many group-living animals, including humans, high social status has clear reproductive benefits (Alberts, 2012; Clutton-Brock, 2016; Ellis, 1995; Majolo et al., 2012; von Rueden and Jaeggi, 2016). Social status also has effects on health and longevity, but the direction and magnitude of these vary across species and between the sexes (Sapolsky, 2004). High-ranking animals typically enjoy preferential access to important resources, such as food, water, safe foraging and sleeping sites, and social support (Krause, 1994; Snyder-Mackler et al., 2016; Stockley and Bro-Jørgensen, 2011). Consequently, rank is generally expected to show positive correlations with health and survival (Snyder-Mackler et al., 2020).

A growing body of evidence, however, suggests that a positive relationship between health and social status is more common among females than males. Across a wide range of vertebrates, dominant males routinely face greater parasitism than subordinates (Habig and Archie, 2015; Habig et al., 2018), and fail to show consistent advantages in longevity (Clutton-Brock, 2016; Creel and Creel, 2002; Hoogland, 1995; McElligott and Hayden, 2000; Robinson et al., 2006; Verhulst et al., 2014). Dominant females, by contrast, routinely outlive subordinates (Creel and Creel, 2002; Robbins et al., 2011; Snyder-Mackler et al., 2020), and fail to show consistently elevated levels of parasitism (Habig et al., 2018).

One explanation for this sex difference is that, in many species, high-ranking males invest considerably more in mating effort than do

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subordinates, and this trades off against investments in somatic maintenance (Rolff, 2002; Stoehr and Kokko, 2006). High-ranking males often maintain energetically expensive armaments, including sexually dimorphic musculature, and engage in energetically expensive behaviors, such as aggressive displays (Clutton-Brock and Huchard 2013; Emery Thompson and Georgiev, 2014; Emlen, 2008; Key and Ross, 1999). They also attract violent challenges from other males, increasing their risk of injury (Clutton-Brock, 2016; Knott and Kahlenberg, 2007; Koren et al., 2008; MacCormick et al., 2011). Among females, escalated fights are generally less frequent, and weapons less highly developed (Clutton-Brock, 2016). Further, fitness gains from high rank are often less pronounced in females, reducing variation in reproductive effort across ranks compared to males (Clutton-Brock and Huchard 2013, Ellis, 1995).

An important mechanism linking social status and health is the glucocorticoid stress response (Sapolsky, 2004, 2005). Glucocorticoids are steroid hormones produced by the adrenal cortex under stimulation from the pituitary. Glucocorticoids interact with insulin to regulate metabolism, increasing blood glucose concentrations, stimulating the release of free fatty acids from adipose tissue, and inhibiting glucose uptake and glycogen synthesis (Arlt and Stewart, 2005; Dallman et al., 1993). Basal glucocorticoid release shows a distinct daily rhythm that is responsive to food consumption (Dallman et al., 1993). In diurnal species a peak generally occurs in the early morning, following the overnight fast, to release stored energy in anticipation of the active period (Oster et al., 2017).

Glucocorticoids are also released at higher concentrations in reaction to noxious or threatening stimuli, as a component of the "classic stress response" (Romero and Wingfield, 2016). Such stimuli come in two broad forms. Physiological (or reactive) stressors are direct, external challenges to homeostasis. Psychosocial (or anticipatory) stressors are indications that an external challenge to homeostasis is forthcoming (Boonstra, 2013; Sapolsky, 2004). Acute increases in glucocorticoid secretion coordinate a range of behavioral and physiological responses that help animals to cope with stressors (Sapolsky et al., 2000). These include changes in metabolism and cardiovascular function that mobilize energy and direct it to skeletal muscle (ibid.). The glucocorticoid stress response is thus critical for promoting short-term survival.

When chronic stressors are present, or acute stressors recur frequently, persistent activation of the hypothalamic-pituitary-adrenal axis can sustain high circulating levels of glucocorticoids. Under these conditions, the same metabolic responses that are protective in the short-term can produce deleterious effects, including atherosclerosis, muscle wasting, and immunosuppression (Romero and Wingfield, 2016; Sapolsky, 1993a). How frequently this condition, termed "homeostatic overload" (Romero et al., 2009), actually occurs in wild animals, as opposed to animals in the laboratory or humans, is unclear (Beehner and Bergman, 2017; Boonstra, 2013; Romero and Wingfield, 2016).

Even under less extreme circumstances, however, there are energetic costs to mounting a stress response (Sapolsky, 1993a). Consequently, frequent exposure to stressors increases the energy needed to preserve homeostasis, curtailing investment in somatic maintenance. Over time this generates wear and tear that reduces an animal's ability to cope with future stressors (Romero et al., 2009; Romero and Wingfield, 2016). This means that even though the stress response is ultimately adaptive (i.e. fitness maximizing), over the long term elevated glucocorticoid production might be associated with increased morbidity or mortality, particularly in long-lived species (Schoenle et al., 2018).

Consistent with the prediction that elevated glucocorticoid levels over time lead to cumulative damage, a recent meta-analysis reported that both baseline and stress-induced glucocorticoid levels showed stronger negative associations with survival in longer-lived species (Schoenle et al., 2021). Experimentally increasing glucocorticoid levels also predictably reduced survival, with stronger effects the longer that survival was monitored (ibid.). Four primate field studies have directly examined the relationship between glucocorticoid exposure and survival, all reporting negative effects. Ring-tailed lemurs (*Lemur catta*) with high fecal glucocorticoid levels showed elevated mortality over a two-year study (Pride, 2005; the only study of these four considered in Schoenle et al., 2021). Vervet monkeys (*Chlorocebus pygerythrus*) that exhibited high fecal glucocorticoid levels under non-drought conditions showed elevated mortality in response to a drought (Young et al., 2019). Gray mouse lemurs (*Microcebus murinus*) with high concentrations of hair cortisol (a measure that averages production across weeks or months) showed elevated mortality, both over time and in response to the breeding season (Rakotoniaina et al., 2017). Finally, in a large, long-term study of wild baboons (*Papio cynocephalus*), females with chronically elevated glucocorticoid levels had shorter lifespans (242 females observed over 1634 female years: (Campos et al., in press).

Early work on social status and health hypothesized that low-ranking animals would generally experience higher glucocorticoid levels than dominants (Sapolsky, 1992). The logic of this *stress of subordination* hypothesis is straightforward. Suboptimal access to resources is expected to produce physiological stress. Decreased predictability and control in social interactions is expected to produce psychosocial stress. This pattern has indeed been observed in a range of vertebrates (Abbott et al. 2003; Blanchard et al., 2001; Sapolsky 1992; Sapolsky, 2005).

In many species, however, dominants maintain higher glucocorticoid levels than subordinates (e.g. cooperative breeders: Creel, 2001, 2005). Among primates, the most intensively surveyed group, more than 60 studies have examined the relationship between rank and glucocorticoid production in the wild (Beehner and Bergman, 2017). These studies reveal a sex difference in rank effects that mirrors the ones previously discussed for parasitism and longevity. Specifically, where rank-related differences have been detected in primates, among females dominants normally show lower glucocorticoid levels than subordinates, whereas among males dominants normally show higher glucocorticoid levels than subordinates (Beehner and Bergman, 2017; Cavigelli and Caruso, 2015).

Why are glucocorticoid levels commonly elevated in high-ranking males? The *costs of dominance* hypothesis posits that rank and glucocorticoid production are positively correlated in contexts where acquiring and maintaining rank are energetically expensive (Creel, 2001; Creel et al., 2013; Goymann and Wingfield, 2004; Muller and Wrangham, 2004b). Aggression is often a salient costly behavior. For example, in species where high-ranking males are habitually more aggressive than other group members, they habitually show elevated glucocorticoid levels (e.g. Arlet et al., 2009; Koren et al., 2008; Muller and Wrangham, 2004b). Other species show positive correlations among rank, aggression, and glucocorticoid production only when hierarchies are unstable and the status of dominant animals is threatened (Sapolsky 1992; Sapolsky, 1993b, 2005; Setchell et al., 2010). And, in some species, high-ranking males are more aggressive than others primarily in mating contexts, leading to a positive correlation between rank and glucocorticoid production when mating opportunities are contested (Mooring et al., 2006; Setchell et al., 2010; Surbeck et al., 2012).

In other cases the mechanism linking high rank and glucocorticoid production is uncertain. In a study of African wild dogs (*Lycaon pictus*), for example, dominants of both sexes showed higher rates of aggression than subordinates only during the mating season, yet maintained elevated glucocorticoid levels throughout the year (Creel, 2005). And, in gray wolves (*Canis lupus*), dominants of both sexes routinely had higher glucocorticoid levels than subordinates, but did not show higher rates of aggression (Creel, 2005). Cooperative breeders like these may represent a special case in which dominants of both sexes invest much more in reproductive effort than do subordinates, not only through aggression, but in ways that are more difficult to measure (ibid.).

Among primates, Cavigelli and Caruso (2015) argue that the high levels of glucocorticoid production observed in dominant males may not have negative effects on health, because they are often transitory. They note that dominant animals show acute peaks of glucocorticoid production during mating competition, or when hierarchies are unstable,

but hypothesize that they quickly return to low baseline levels. Subordinates, by contrast, are hypothesized to regularly maintain high baseline glucocorticoid levels, even if their acute reactions to competition are muted. Such chronic stress is expected to have stronger adverse effects on health. In practice this *acute costs of dominance, chronic stress of subordination* hypothesis has rarely been tested, as it requires sufficient longitudinal data on individuals to distinguish short-term elevations in glucocorticoid production from long-term baseline levels. Limited evidence suggests that it may apply to female ring-tailed lemurs (*Lemur catta*), which maintain a short (1–3 week) annual breeding season in the wild (Cavigelli and Caruso, 2015; Sauther et al., 1999).

In this paper we use 20 years of longitudinal data on male chimpanzees (*Pan troglodytes schweinfurthii*) living in the Kanyawara community, Kibale National Park, Uganda, to examine the relationship between glucocorticoid production and social status. Male chimpanzees are interesting because they generally form despotic, linear dominance hierarchies in which rank is frequently contested through aggression (Goodall, 1986; Muller, 2002), sometimes lethally (Fawcett and Muhumuza, 2000; Kaburu et al., 2013; Pruetz et al., 2017; Wilson et al., 2014). Males also fight over access to estrous females, who do not breed seasonally, but are available unpredictably throughout the year (Goodall, 1986; Muller, 2017b; Muller and Mitani, 2005). Dominant males gain clear reproductive benefits and enjoy priority of access to food (Boesch et al., 2006; Goodall, 1986; Newton-Fisher et al., 2010; Pusey et al., 2005; Wroblewski et al., 2009). However, in Kanyawara they also maintain lower levels of urinary C-peptide (a biomarker of insulin production) than subordinates, suggesting energetic costs to maintaining rank (Emery Thompson et al., 2009).

Previous studies of social status and glucocorticoid production in chimpanzees have drawn mixed conclusions. Our own early studies in Kanyawara documented the same sex difference observed among primates generally. In a six-year study of females, dominant individuals showed lower glucocorticoid levels than subordinates, an effect that was strongest during the energetically costly period of lactation (Emery Thompson et al., 2010). And, in a one-year study of males, glucocorticoid production, aggression, and rank were positively correlated, with males showing increases in aggression and glucocorticoid production when competing over sexually receptive females (Muller and Wrangham, 2004b). We did not, however, quantify stability of the dominance hierarchy, nor address the issue of acute versus chronic increases in glucocorticoid production.

By contrast, two subsequent studies reported no relationship between rank and glucocorticoid production in male chimpanzees. The first, a short 3-month study in the Ngogo community, Kibale National Park, is difficult to interpret. It involved a stable dominance hierarchy, but relied on a small number of samples (1–5 per individual), and did not report whether any of these were collected in the presence of sexually receptive females (Muehlenbein and Watts, 2010).

The second, a recent study in Ivory Coast, is more puzzling (Preis et al., 2019). Two chimpanzee communities in Taï National Park were studied for ~17 months, during which 983 urine samples were collected from 10 males. Unsurprisingly, males showed elevated glucocorticoid production during periods of dominance instability, and in the presence of estrous females. However, glucocorticoid levels were associated neither with dominance rank nor with aggression. Oddly, there was no increase in aggression during the periods of dominance instability. This might partly be due to the unusual demographic composition of the Taï communities during the study. Because of recent high mortality, only 2 fully adult males were present in one community, and 3 in the other, for the complete study period. The remaining males were adolescents for all or part of the study. It is plausible that a high-ranking male in a community containing only 1–2 other adult males will experience less uncertainty surrounding dominance interactions than males in a larger group.

However, it is also possible that the Taï study systematically underestimated the glucocorticoid levels of fully adult males, in relation to adolescents, by indexing glucocorticoid measurements to creatinine. Urinary steroids are frequently indexed to creatinine, which is produced at a relatively constant rate by muscle tissue, to correct for variation in fluid intake and urine concentration (Miller et al., 2004). This procedure can mislead, however, when individuals show differences in creatinine production resulting from differences in muscle mass (Emery Thompson et al., 2012). For this reason, among others, a specific gravity correction for urine concentration is preferable when age-sex classes are compared (Anestis et al., 2009; Miller et al., 2004; White et al., 2010). Because adolescent males ages 9–15 years at Taï were still developing musculature, as indicated by increasing creatinine over time (Samuni et al., 2020), the creatinine correction would have inflated their glucocorticoid measures in relation to larger adults. And, if adolescent males tended to be low ranking, this would have obscured any relationship between rank and glucocorticoid excretion.

Here we examine glucocorticoid levels assayed from 8029 urine samples collected from 20 adult males in the Kanyawara community, Kibale National Park, over two decades (December 1997 through May 2017). These long-term endocrine data allowed us to look at the effects of mating opportunity, food availability, aggression, instability in the dominance hierarchy, and other factors on glucocorticoid levels both within and between individuals over time. The primary goal was to identify the major stressors that drive glucocorticoid production in male chimpanzees, and to examine how these interact with rank. We predicted that low food availability would disproportionately increase glucocorticoid production in low-ranking males, as they are likely to be displaced from the best feeding locations. We predicted that instability in the dominance hierarchy and competition over mating opportunities would disproportionately increase glucocorticoid levels in dominant individuals, since their status would be at risk, and they invest more in mating effort. Finally, we predicted that aggression would be a critical mechanism linking glucocorticoid production with rank, instability, and mating opportunity (Muller and Wrangham, 2004b).

Our secondary goal was to distinguish among (1) the *stress of subordination* hypothesis, (2) the *costs of dominance* hypothesis and (3) the *acute costs of dominance/chronic costs of subordinance* hypothesis. The first posits that subordinate males show chronically elevated glucocorticoid levels, owing to a lack of social predictability and control, and reduced access to high-quality food. The second posits that high-ranking males show chronically elevated glucocorticoid production, owing to their investments in maintaining rank and competing for mates, and that this represents a cost of mating effort. The third predicts that baseline glucocorticoid levels will be higher in subordinates than in dominants, after controlling for the acute elevations that may occur in response to short-term challenges.

2. Methods

Chimpanzees in the Kanyawara community, Kibale National Park, southwestern Uganda, were first studied systematically from 1983 to 1985, and have been continuously monitored by the Kibale Chimpanzee Project (KCP) since 1987 (Isabirye-Basuta, 1988; Muller and Wrangham, 2014). The Kanyawara chimpanzees were habituated without provisioning, and observations were conducted with a minimum observer distance of five meters. Over the main study period, from late 1997 to early 2017, the community comprised 49–54 chimpanzees, including 9–11 adult males and 13–18 adult females.

Struhsaker (1997) provides a detailed description of the study site. All research was conducted with the approval of the Institutional Animal Care and Use Committees of Harvard University, Tufts University, and the University of New Mexico.

Behavior was recorded by a team of observers, which normally consisted of 2–3 long-term Ugandan field assistants and 1–2 university-based researchers. Whenever possible, observers followed chimpanzees from the time that they woke in the morning until they constructed their night nests. Chimpanzees were usually located at the site where they had

nested the previous evening, but also by following their tracks, listening for calls, and waiting near fruiting trees. Because chimpanzees exhibit fission-fusion grouping, multiple teams sometimes followed different chimpanzee parties simultaneously. A party was defined as all chimpanzees within 50 continuous meters of each other.

This study draws on three sets of long-term data. (1) Dominance ranks were calculated from a combination of ad libitum and all-occurrence sampling data (Altmann, 1974) collected between January 1993 and June 2017. (2) Endocrine data came from urine samples collected between November 1997 and May 2017. These were matched with behavioral data, including 15-min scan sampling of party composition and group-level feeding behavior, collected over 6538 study days and 75,212 h of observation. (3) Detailed, all-occurrence sampling data on aggression were available from January 2005 to May 2017. These included 4316 unique study days and 55,484 h of observation. Confidence in the accuracy of the long-term behavioral data comes from tests documenting close agreement between focal data collected by researchers and all-occurrence sampling data collected independently by field assistants, together with routine measures of inter-observer reliability (Muller et al., 2007; Gilby et al., 2010).

2.1. Hormone methods

To quantify rates of glucocorticoid excretion, we assayed 8029 urine samples collected non-invasively from 20 individuals (mean: 401.5 samples/male, range: 17–1395) between November 1997 and May 2017 (Table 1). We considered only adult males (those 15 years or older) in our analyses, as they were physically, socially, and sexually mature.

When a chimpanzee urinated from a tree, observers trapped urine on a disposable plastic bag attached to a two-meter pole. If a bag could not be placed in time, then urine was pipetted from leaves in the ground layer of vegetation. To minimize the risk of sample cross-contamination, urine was collected from vegetation only when it was clear that multiple individuals had not urinated in the same area. Care was also taken to avoid collecting urine contaminated with feces. Immediately after collection, the identity of the chimpanzee, the date, and the time of urination were recorded, and samples were placed in a thermos bottle containing a cold pack. Samples were frozen at approximately −20 °C at the end of the daily follow (within 14 h). Later they were transported on ice to the U.S., in compliance with U.S. Centers for Disease Control and World Health Organization regulations. Muller and Wrangham (2004b) provide additional details on the validation of sample collection procedures.

Table 1
Sample sizes by male ID.

Male	Ages	Urine samples (1997–2017)	Observation hours (2005–2017)	Months (Models 2–3)	Months 2 (Model 4)
AJ	23–40	529	8123	69	51
AT	15–17	308	4516	29	26
BB	31–50	496	8526	75	54
BF	31–32	17	0	0	0
ES	15–22	477	9274	70	54
KK	15–27	873	11,391	80	73
LB	29–32	133	0	0	0
LK	15–33	1395	16,601	122	112
MS	22–35	435	5916	48	37
MX	15–19	149	3161	34	30
OG	15–16	110	1555	12	12
PB	15–22	451	7525	65	57
PG	15–24	530	4939	41	36
SL	26–33	73	284	2	2
ST	42–57	355	3784	38	28
SY	33–35	84	0	0	0
TJ	15–21	390	6825	65	59
TT	15–16	136	2103	16	14
TU	37–53	261	5425	48	32
YB	24–43	827	11,060	96	66
Total		8029	111,008	910	743

"Months" indicates the number of months in which a male was observed for at least 15 h (Models 2–3). "Months 2" indicates the number of months in which a male was observed for at least 15 h and provided at least 2 urine samples (Model 4).

Immunoreactive glucocorticoids were measured using enzyme-immunoassay reagents and protocols provided by the Clinical Endocrinology Laboratory at the University of California at Davis (polyclonal rabbit anti-cortisol R4866: Munro and Lasley, 1988). This assay has been widely validated and used across taxa for the assessment of glucocorticoids in urine and other media (for chimpanzees: Kahlenberg et al., 2008, Muller et al., 2007). Intra-assay CV, calculated as the average CV between duplicate determinations, was 7.1%. Due to the longitudinal nature of our study, samples were assayed at intervals between 2005 and 2018, involving the same assay protocol but two different laboratories at Boston University (2005–2007) and the University of New Mexico (2008–2018). We employed iterative cross-validations, using pooled urine samples as controls, to ensure replicability of the assay over time (for details see Sabbi et al., 2020). Briefly, inter-assay CVs of all assays (i.e. across labs) were 13.4% and 12.5% for low and high controls, respectively, while the CV of mean values between labs was 7.3% for the low control and 5.0% for the high control. While these assays required using two different lots of reagents (A: 2005–2015, B: 2015–2018), these performed nearly identically (inter-low CVs: low control 1.6%, high control 0.1%). While this suggests that our assay performed consistently over time, we entered a random variable for the year of assay to address potential variation due to differences in laboratories, reagents, or equipment. This procedure improved model fit but did not alter overall findings relative to modeling that omitted this random effect.

All samples were assayed within ten years of collection, and 78% were analyzed within 5 years (mean interval = 3.3 years). To control for the possibility of glucocorticoid degradation over time (for discussion see Emery Thompson et al., 2020), we included a variable in our models for time between sample collection and assay (0–4 years, 4–7 years, 7–10 years). To control for the dilution of analytes by water, we corrected all results for specific gravity, measured with a handheld refractometer (Atago PAL—10S). This correction took the original glucocorticoid value and divided it by $(SG_s\text{-}1)/(SG_X\text{-}1)$ where SG_s was the specific gravity of the sample and SG_X was the average sample specific gravity across the population (Buchwald, 1964). Corrected values were natural log-transformed prior to statistical analysis.

2.2. Behavioral data

Four categories of behavior constituted male aggression. *Stationary threats* consisted of an arm wave at the victim, without locomotion. *Charging displays* involved exaggerated locomotion, piloerection, and sometimes branch dragging or shaking. Displays could be targeted toward specific individuals (directed charges), or the group in general (non-directed displays). *Chases* were recorded when a male pursued a fleeing individual, who was generally screaming. All incidents of contact aggression were recorded as *Attacks*. These included hits, kicks, or slaps delivered in passing, as well as extended episodes of pounding, dragging, and biting (Goodall, 1986; Muller, 2002; Muller and Wrangham, 2004a). Chases and attacks were classified as high-level aggression, whereas charges and stationary threats were considered low-level aggression (as in Preis et al., 2019). We focused on high-level aggression when testing the effects of received aggression on glucocorticoids, because in some cases it was unclear whether low-level aggression was directed at a specific individual. Chases and attacks were visibly distressing to unambiguous victims.

Chimpanzee aggression involved exaggerated movements by the perpetrators and loud vocalizations (e.g. screams or waa barks) from the victims, rendering it highly conspicuous to observers. Thus, our record of aggression is equivalent to all-occurrence sampling (Altmann, 1974). Nevertheless, the long-term data underestimate true rates of aggression,

because some interactions are obscured by vegetation, such that the identities of aggressors or victims cannot be confirmed. Muller et al. (2007) compared focal data on aggression collected by a single observer with long-term data, and showed that these underestimates represent an unbiased sample of the behavior.

Rates of individual male aggression were calculated for each month of the study from 2005 to 2017 in which a male was observed for a minimum of 15 h (monthly average = 121.8 h, range = 15.25–364.75). This resulted in a sample of 910 chimpanzee months from 17 unique males (average = 53.5 months per male, range = 2–122, Table 1). Rates were based on the number of discrete aggressive events that a male participated in during the period of observation, classified by the most extreme form of aggression observed in the event. For example, if a male charged at another individual, and immediately chased that individual and attacked him, this would have been scored as a single event - an attack. If two separate individuals were attacked, this would have been scored as two events. If, after an episode of aggression, a male engaged in some other behavior for at least one minute, subsequent aggression was assigned to a new event.

Male dominance ranks were determined from 13,415 dyadic interactions among 27 males, spanning January 1993 through June 2017. Wins and losses were assigned based on the directionality of pant-grunts (a formal signal of subordination), and submissive responses to received aggression (e.g. screaming and fleeing). An Elo rating method was used to assign relative ranks on each day of the study period for males 9 and older (Albers and De Vries, 2001; Neumann et al., 2011). Males in 1993 were assigned a starting score of zero, and males that reached adolescence (beginning at age 9) during the study period were assigned a starting score one point below the lowest-ranking male in the hierarchy on the day of their first aggressive interaction with an adult male. The k-constant in the Elo rating equation was set to 20. Elo scores were ultimately transformed into ordinal ranks, which were standardized for the number of males in the community (standardized rank = (n − r) / (n − 1), where n is the number of adult males in the hierarchy and r is a male's ordinal rank in the hierarchy. Thus, the alpha male always had the highest rank score of 1, with other adult males falling between 0 and 1. Because dominance data were available from 1993, a burn-in period of almost 5 years ensured that reliable ranks were established for males before the onset of urine sampling in late 1997.

Hierarchy stability was assayed using Elo scores. Whenever there was a rank reversal between two adult males, we considered the 4 weeks prior to the day of the reversal a period of instability in the hierarchy at the group level. (In order to assess stability, our dominance data necessarily extend one month beyond our other datasets.) To test whether direct involvement in a rank reversal was predictive of increased glucocorticoid production, in some analyses the hierarchy was considered unstable specifically for the two individuals involved in the rank reversal (again, for 4 weeks prior to the day of the reversal).

We employed a simple scale to record the degree of tumescence of the sexual swelling for each adult female in a party (e.g. Wallis, 1992). Females with sexual skins that were completely flat received scores of (1) *no swelling*. Females with sexual skins that were partly inflated, but wrinkled and droopy, received scores of (2) *partial swelling*. Females with sexual skins that were fully expanded (i.e. tense and shiny with no drooping) received scores of (3) *maximally tumescent*. Previous studies in Kanyawara have shown that adult males show little interest in monopolizing nulliparous females, but are strongly attracted to parous females with maximally tumescent sexual swellings (Muller et al., 2006; Muller et al., 2007; Muller and Wrangham, 2004a). Consequently, we considered whether males were in parties containing at least one maximally-tumescent, parous female.

2.3. Dietary quality

Kanyawara chimpanzees eat ripe fruit in proportion to its availability (Wrangham et al., 1998). Because fruit abundance varies temporally, chimpanzees are occasionally forced to fall back on lower quality piths and herbs, which are more widely distributed through the study site (Wrangham et al., 1991; Conklin-Brittain et al., 1998). Thus, when fruit is scarce, the Kanyawara chimpanzees subsist on a diet that is significantly lower in simple sugars, non-structural carbohydrates, and fat, than when fruit is abundant (Conklin-Brittain et al., 1998). These periods of low fruit availability represent times of increased energetic stress (Emery Thompson et al., 2014; Emery Thompson et al., 2009).

Observers noted at 15-min intervals whether chimpanzees in the party under observation were feeding. If they were, both the species and portion of the plant being consumed by the majority were recorded. Dietary quality was estimated by calculating the total percentage of feeding observations in which chimpanzees consumed fruit. This measure has previously been shown to correlate with direct estimates of fruit abundance from phenology transects (Wrangham et al., 1996).

2.4. Age estimation

Individuals who were born before the study began were assigned ages by comparing their physical and behavioral characteristics with those of chimpanzees of known ages. Young adult chimpanzees (15–20 years old) exhibit a suite of morphological characteristics that include thick glossy black hair, unbroken teeth, and light facial creasing. Chimpanzees older than 35 years display thinning brown or gray hair with less sheen, worn or broken teeth, and saggy, wrinkled faces. These individuals also move more slowly and deliberately. Female ages were further calibrated based on the apparent ages of their offspring. Hill et al. (2001) provide additional details on estimating the ages of wild chimpanzees in these study sites. Of the males in this sample: 9 were born during the study period and have known ages, 4 were immature when first identified and have narrow age estimates, and 7 were adults when the study began and were at least 29 years old by the time of first sampling.

2.5. Data analysis

2.5.1. Urinary glucocorticoid model (1)

The response variable in this model was a single urinary glucocorticoid measurement (natural log-transformed cortisol ng/ml corrected for specific gravity, n = 8039, Table 1). We fitted a linear mixed model (LMM) to examine the effects of dominance rank, hierarchy stability, and mating opportunity on urinary glucocorticoids. For each value, key predictors were male rank on the day of sampling (from 0 to 1), hierarchy stability at the group level (stable or unstable), presence or absence of parous estrous females (one or more present in the party when the urine sample was collected or not), and dietary quality over the 14 days prior to sampling (% feeding scans in which chimpanzees were eating ripe fruit). Previous studies of baboons revealed that alpha status was a better predictor than ordinal rank of glucocorticoid production in males (Gesquiere et al., 2011), so we also included this as a variable (alpha or non-alpha). We further assessed dominance stability at the individual level, to test whether males who were directly involved in dominance reversals showed elevated glucocorticoids during periods of instability compared with those who were not. Specifically, when there was a rank reversal between two males, the preceding four weeks were considered unstable for those males, but not for other males in the community.

Because glucocorticoid production shows a diurnal pattern, with the highest levels in the morning and a decrease through the day (Muller and Lipson, 2003), we included time of urination as a control predictor. We further controlled for chimpanzee age and years between urine collection and assay. To control for variation in sampling across individuals and over time, we included chimpanzee ID as a random effect. A random slope was also included for dominance rank, when it was used as a fixed effect. Year of assay was included as a random effect (SI Appendix).

We tested whether males of different status varied in their glucocorticoid responses to mating opportunity and dominance instability by introducing six interactions. These combined our two measures of rank (ordinal and alpha/non-alpha) with two measures of instability (group level and individual level) and one of mating opportunity (presence/absence of parous estrous females). Finally, we tested whether high- and low-ranking males differed in their glucocorticoid response to food availability by introducing interactions between our measure of dietary quality and our two measures of rank.

2.5.2. Aggression models (2–3)

The target variable in these models was a monthly count of either aggression given or aggression received for an individual adult male (n = 910 male months, 17 unique males, Table 1).

Model 2. To examine the effects of dominance rank, hierarchy stability, and mating opportunity on the incidence of male aggression, we fitted a generalized linear mixed model (GLMM) using a negative binomial distribution with a log link function. Aggression data were monthly counts, with an offset for the number of 15-min scans in which a male was observed during the month (logged). Key predictors were average male rank for the month (from 0 to 1), hierarchy stability (percentage of unstable days during the month, at the group level), and mating opportunity (percentage of 15-min scans during the month in which the male was in a party with one or more estrous females). As in Model 1, we controlled for male age during the month and dietary quality (% feeding scans in which chimpanzees were eating ripe fruit). Chimpanzee ID was included as a random effect, and a random slope was introduced for dominance rank.

Finally, we introduced two interactions to test whether high- and low-ranking males differed in their aggressive response to hierarchy instability (rank * stability) and mating opportunity (rank * percentage scans with parous estrous females).

Model 3. This was identical to Model 2, except the target variable was high-level aggression received (chases and attacks) instead of aggression given.

2.5.3. Monthly aggression and glucocorticoid model (4)

The response variable in this model was an average monthly glucocorticoid value for an individual male (n = 743 male months, 17 unique males, Table 1). Individual values were time-corrected by calculating residuals from the relationship of glucocorticoids against the time of urination (Emery Thompson et al., 2020).

We fitted a linear mixed model (LMM) to examine the effects of dominance rank, hierarchy stability, presence of estrous females, and aggression given and received on urinary glucocorticoid levels. Key predictors were average male rank for the month (from 0 to 1), hierarchy stability (percentage of unstable days during the month, at the group level), mating opportunity (percentage of 15-min scans during the month in which the male was in a party with one or more parous estrous females), aggression given (rate of male aggression given during the month), high-level aggression received (rate of chases and attacks experienced by a male in the month), and dietary quality (% feeding scans in which chimpanzees were eating ripe fruit). As in Models 1–3, we controlled for male age, chimpanzee ID was included as a random effect, and a random slope was introduced for dominance rank.

All models were constructed in R using the *lmer* function in the *lme4* package. Continuous predictors were centered on the mean, except for age (centered at 15 years) and time of urination (centered at 12 pm). Statistical significance of fixed effects was determined using type III Wald Chi-square tests, and significance of random effects was determined with log-likelihood ratio tests (LLRT) by dropping one term at a time. Diagnostic plots of models 1 and 4 (LMMs) were evaluated to verify that residuals were uncorrelated and distributed normally. All variance inflation factors were <2, indicating no concerns with multicollinearity.

3. Results

Fig. 1 shows Elo ratings for males from January 1993 to June 2017, which includes the initial burn-in period. From November 1997, when urine collection began, through June 2017, there were 145 rank reversals between adult males. Out of 7152 days, the hierarchy was classified as stable in 4619 (65%) and unstable in 2533 (35%). Distinct periods of stability are evident in Fig. 1; for example, from mid-2001 to early 2003 there were no dominance reversals. There are also visible periods of churn, such as most of 2006.

3.1. Urinary glucocorticoid model

Output from the full urinary glucocorticoid model is presented in the supplement (Table S1). Instability (group-level) by rank was the only significant interaction, so all others were omitted from the final model. Because there was no discrete effect of being alpha male, or of dominance instability at the individual level, these predictors were also omitted, to clarify the effects of ordinal rank and dominance instability at the group level. All other predictors and controls were included in the final model (Table 2).

Overall, urinary glucocorticoid levels in male chimpanzees increased with increasing rank (estimate = 0.494, SE = 0.168, χ^2 = 8.6, P = 0.003). This was true in both stable and unstable dominance hierarchies, and in both mating and non-mating contexts (Fig. 2). Alpha male status had no distinct impact on urinary glucocorticoids.

As predicted, mating opportunity had a large effect on male glucocorticoid levels. Across ranks, males exhibited increased glucocorticoid excretion in the presence of parous estrous females (estimate = 0.176, SE = 0.013, χ^2 = 171.4, P < 0.001).

Instability in the dominance hierarchy was also associated with male glucocorticoids, but this relationship changed with rank (estimate = 0.122, SE = 0.044, χ^2 = 7.8, P = 0.005). The lowest-ranking males showed no difference in glucocorticoid excretion between stable and unstable periods (Fig. 2). With increasing rank, however, males showed larger glucocorticoid responses to instability. These effects were all limited to instability at the group level. There was no discrete effect of instability at the individual level.

As previously reported from this population (Emery Thompson et al., 2020), glucocorticoids increased with male age (estimate = 0.008, SE = 0.003, χ^2 = 8.0, P = 0.005). Dietary quality, defined as the proportion of ripe fruit in the chimpanzees' diet in the previous 14 days, did not influence male glucocorticoid concentrations, alone (estimate = −0.012, SE = 0.072, χ^2 = 0.03, P = 0.873) or in interaction with rank.

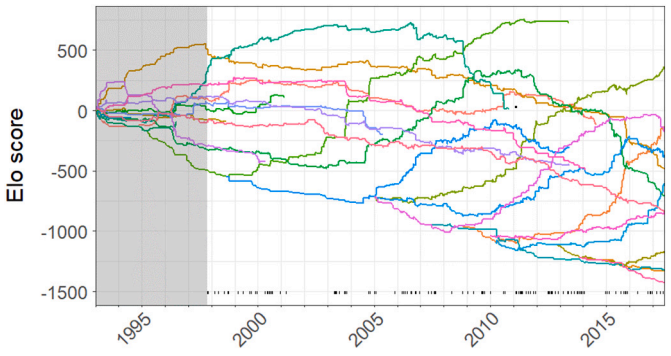

Fig. 1. Male chimpanzee dominance trajectories. The colored lines show Elo ratings over time for individual male chimpanzees (n = 13,415 dyadic interactions), with scores indicating relative male status. Tick marks at the bottom indicate dates on which rank reversals (n = 145) occurred between adult males. The shaded area shows a burn-in period, prior to the initiation of urine sampling in December 1997.

Table 2
Predictors of male glucocorticoids (Model 1).

Term	Estimate	Variance	SE	SD	χ^2	P
Intercept	10.867		0.083		17,008.6	<0.001
Test						
Rank	0.494		0.168		8.6	0.003
Instability	0.042		0.012		12.5	<0.001
Estrous females	0.176		0.013		171.4	<0.001
Ripe fruit	−0.012		0.073		0.03	0.873
Rank * Instability	0.122		0.044		7.8	0.005
Controls						
Age	0.008		0.003		8.0	0.005
Time of day	−0.144		0.003		2202.5	<0.001
Years to assay					591.6	<0.001
4–6 y	−0.650		0.030			
7–9 y	−0.736		0.042			
Random effects						
Chimp ID		0.016		0.125	64.6	<0.001
Rank * Chimp ID		0.364		0.603	24.4	<0.001
Year of assay		0.030		0.172	15.6	<0.001

n = 8029 urine samples, 20 males. Significance of fixed effects was determined via type III Wald chi-square tests. Significance of random effects and interactions was determined via LLRTs.

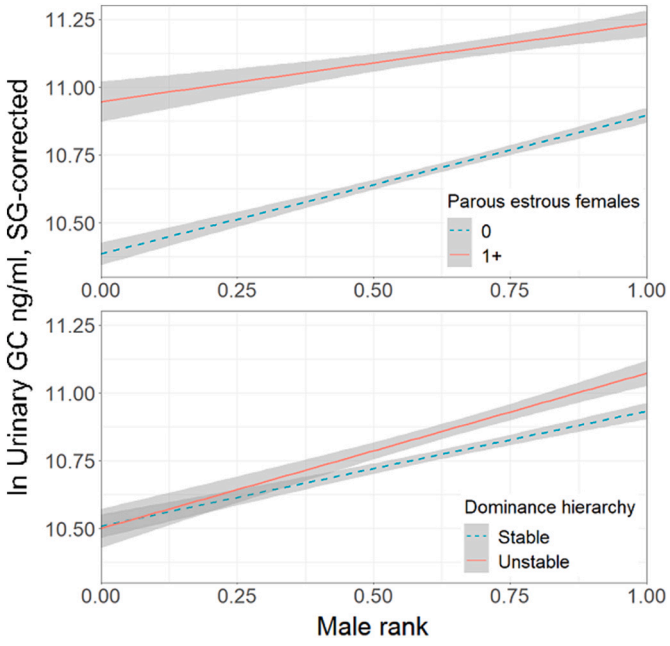

Fig. 2. Glucocorticoid (GC) levels by dominance rank in male chimpanzees (n = 8029 samples, 20 adults). Both the presence of parous estrous females (top panel) and instability in the dominance hierarchy (bottom panel) were associated with increased glucorticoid production in male chimpanzees. Instability had a greater effect on the glucocorticoids of higher-ranked males. The shaded areas indicate 95% confidence intervals. (Fig. S1 plots the same data showing individual points.)

3.2. Aggression models

Output from the full aggression models is presented in Tables 3 and 4. The strongest predictors of male aggression largely mirrored those of glucocorticoids. Overall, high-ranking males were more aggressive than low-ranking males (estimate = 1.353, SE = 0.353, z = 3.83, P < 0.001). This was true in both stable and unstable hierarchies, and in both mating and non-mating contexts (Fig. 3).

Mating opportunity had a substantial effect on male aggression rates

Table 3
Predictors of monthly aggression given (Model 2).

Term	Estimate	Variance	SE	SD	z	P
Intercept	−1.356		0.105		−12.93	<0.001
Test						
Rank	1.353		0.353		3.83	<0.001
Instability	0.185		0.047		3.93	<0.001
Estrous females	−0.028		0.060		0.47	0.636
Rank * Estrous females	1.083		0.266		4.08	<0.001
Rank * Instability	0.288		0.201		1.43	0.152
Controls						
Age	−0.028		0.005		−5.49	<0.001
Ripe fruit	0.070		0.114		0.61	0.540
Random effects						
Chimp ID		0.068		0.260	300.41	<0.001
Rank * Chimp ID		1.384		1.176	21.75	<0.001

n = 910 male months, 17 unique males. Significance of fixed effects was determined via type III Wald chi-square tests. Significance of random effects and interactions was determined via LLRTs.

Table 4
Predictors of monthly aggression received (Model 3).

Term	Estimate	Variance	SE	SD	z	P
Intercept	−3.910		0.101		−38.67	<0.001
Test						
Rank	−1.470		0.253		−5.80	<0.001
Instability	0.375		0.082		4.56	<0.001
Estrous females	0.728		0.099		7.34	<0.001
Rank * Estrous females	1.636		0.411		3.98	<0.001
Rank * Instability	0.626		0.334		1.87	0.061
Controls						
Age	0.004		0.005		0.80	0.422
Ripe fruit	0.021		0.202		0.10	0.918
Random effects						
Chimp ID		0.044		0.211	29.92	<0.001
Rank * Chimp ID		0.223		0.472	1.40	0.237

n = 910 male months, 17 unique males. Significance of fixed effects was determined via type III Wald chi-square tests. Significance of random effects and interactions was determined via LLRTs.

that was structured by rank (estimate = 1.083, SE = 0.266, z = 4.08, P < 0.001). The lowest-ranking males did not show increased aggression during months in which they spent more time with parous estrous females (Fig. 3). With increasing rank, however, males showed increasing aggression in months with more mating days. Males were more aggressive during months containing more days with an unstable hierarchy (estimate = 0.185, SE = 0.047, z = 3.93, P < 0.001).

Adult males became less aggressive with increasing age (estimate = −0.028, SE = 0.005, z = −5.49, P < 0.001). Dietary quality was not associated with aggression given, when other predictors were accounted for (estimate = 0.070, SE = 0.114, z = 0.61, P = 0.540).

Predictors of received aggression, in the form of chases and attacks, followed the same pattern as aggression given, but the effect of dominance rank was reversed. Specifically, high-ranking males received less aggression than low-ranking males, in both stable and unstable hierarchies, and in both mating and non-mating contexts (estimate = −1.470, SE = 0.253, z = −5.80, P < 0.001; Fig. 4). Across ranks, males received more aggression in months containing more days with an unstable hierarchy (estimate = 0.375, SE = 0.082, z = 4.56, P < 0.001).

All males received more aggression during months in which they spent more time in parties with parous estrous females (estimate = 0.728, SE = 0.099, z = 7.34, P < 0.001). This interacted with rank,

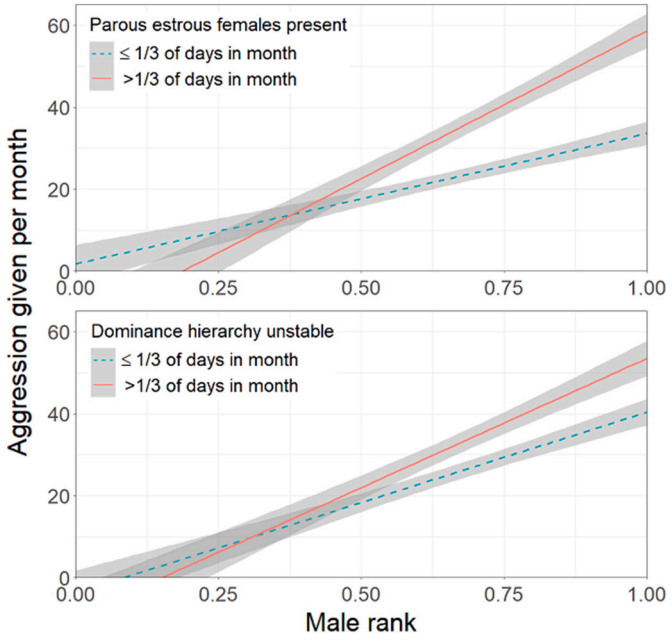

Fig. 3. Monthly aggression given by male chimpanzees by rank (n = 910 months, 17 adults). Across contexts, high-ranking males were more aggressive than low-ranking males. Males were more aggressive in months when they associated more with parous estrous females (top panel) and in months with more days of instability in the dominance hierarchy (bottom panel). Parous estrous females had a greater effect on the amount of aggression given by higher-ranked males. Counts were based on a mean monthly observation time of 122 h. Although instability and presence of estrous females were continuous variables in the models, for visualization purposes they are shown here as categorical variables. The shaded areas indicate 95% confidence intervals. (Fig. S2 plots the same data showing individual points.)

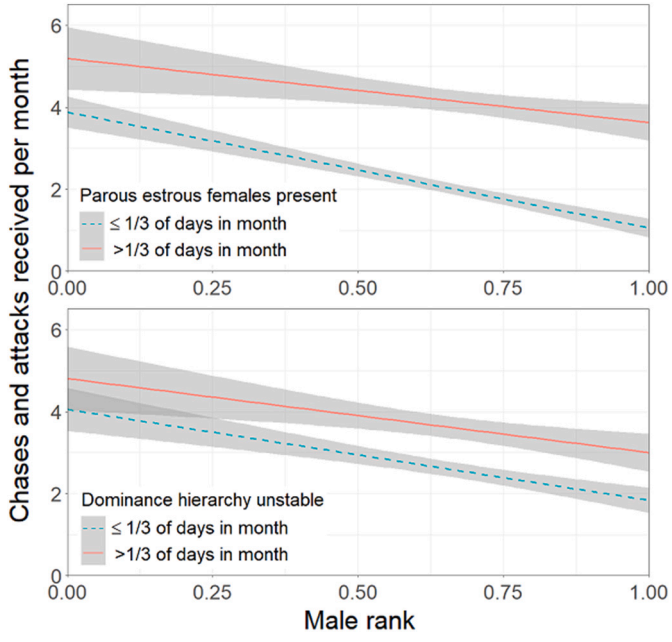

Fig. 4. Monthly aggression received by male chimpanzees by rank (n = 743 months, 17 adults). Across contexts, high-ranking males received less aggression than low-ranking males. Males received more aggression in months when they associated more with parous estrous females (top panel) and in months with more days of instability in the dominance hierarchy (bottom panel). Parous estrous females had a greater effect on the amount of aggression received by higher-ranked males. Counts were based on a mean monthly observation time of 126 h. Although instability and presence of estrous females were continuous variables in the models, for visualization purposes they are shown here as categorical variables. The shaded areas indicate 95% confidence intervals. (Fig. S3 plots the same data showing individual points.)

however, such that the increase was greater for higher-ranked males (estimate = 1.636, SE = 0.411, z = 3.98, P < 0.001, Fig. 4).

Male age was not associated with high-level aggression received (estimate = 0.004, SE = 0.005, z = 0.80, P = 0.422), nor was dietary quality (estimate = 0.021, SE = 0.202, z = 0.10, P = 0.918).

3.3. Monthly aggression and glucocorticoids model

Output from the full model is presented in Table 5. Neither dominance rank (estimate = 0.132, SE = 0.262, $\chi^2 = 0.25$, P = 0.615) nor the number of days with an unstable hierarchy (estimate = −0.053, SE = 0.061, $\chi^2 = 0.75$, P = 0.386) was a significant predictor of mean monthly glucocorticoid values when aggression rates were included as predictors in the model. By contrast, the proportion of observations in association with parous estrous females continued to have a strong effect on mean monthly glucocorticoid values (estimate = 0.644, SE = 0.079, $\chi^2 = 66.2$, P < 0.001). Males showed elevated glucocorticoids during months in which they were more aggressive (estimate = 0.417, SE = 0.177, $\chi^2 = 5.56$, P = 0.018), and also during months in which they received more aggression (estimate = 1.972, SE = 0.961, $\chi^2 = 4.21$, P = 0.040). Glucocorticoids increased with male age (estimate = 0.008, SE = 0.004, $\chi^2 = 3.86$, P = 0.049), but were not influenced by dietary quality (estimate = −0.170, SE = 0.174, $\chi^2 = 0.96$, P = 0.328).

In a final model, we looked at the same predictors and controls, but collapsed aggression given and high-level aggression received into a single variable - monthly rate of involvement in aggression. The results mirror those just discussed (Table S2).

Table 5
Predictors of monthly mean glucocorticoids in male chimpanzees (Model 4).

Term	Estimate	Variance	SE	SD	χ^2	P
Intercept	6.261		0.072		7465.5	<0.001
Test						
Rank	0.132		0.262		0.3	0.615
Instability	−0.053		0.061		0.8	0.386
Estrous females	0.644		0.079		66.2	<0.001
Ripe fruit	−0.170		0.174		1.0	0.328
Aggression given	0.417		0.177		5.6	0.018
Aggression received	1.972		0.961		4.2	0.040
Controls						
Age	0.008		0.004		3.9	0.049
Years to assay					55.8	<0.001
4–6 y	−0.399		0.057			
7–9 y	−0.449		0.133			
Random effects						
Chimp ID		0.019		0.138	16.3	<0.001
Rank * Chimp ID		0.603		0.776	10.7	0.001

n = 743 male months, 17 males. Significance of fixed effects was determined via type III Wald chi-square tests. Significance of random effects and interactions was determined via LLRTs.

4. Discussion

Across two decades in Kanyawara, dominant males showed chronically elevated glucocorticoid levels. In contrast with yellow baboons (Gesquiere et al., 2011), this effect was not restricted to the alpha male. Rather, glucocorticoids were positively associated with ordinal rank in both stable and unstable hierarchies, and in the presence and absence of estrous females. These findings support the *costs of dominance* hypothesis over the *stress of subordination* hypothesis. For chimpanzee males, acquiring and maintaining rank was energetically expensive,

imposing persistent physiological costs that subordinates were able to avoid. The fact that a positive association between glucocorticoids and rank persisted even when controlling for prominent short-term stressors, such as rank instability and the availability of estrous females, is evidence against the *acute costs of dominance/chronic costs of subordinance* hypothesis.

Both giving and receiving aggression were associated with increased glucocorticoid production. Per incident, receiving high-level aggression was a more potent stressor, corresponding to a five-fold increase in glucocorticoids compared to giving aggression (Table 5). However, males gave aggression, primarily in the form of costly dominance displays, around ten times as often as they were chased or attacked. Consequently, aggression given explained more of the total variance in glucocorticoid excretion.

Giving aggression was also the primary mechanism linking glucocorticoids with rank. Dominant males received less high-level aggression than subordinates, but the absolute difference across ranks was modest. For aggression given, by contrast, dominants routinely showed markedly higher rates than subordinates, regardless of hierarchy stability or mating opportunity. When aggression given, aggression received, and rank were included in the same model (Table 5), only the aggression terms were predictive of mean monthly glucocorticoid levels.

Why is aggression so stressful? In part, this likely reflects direct metabolic costs. The most frequent form of chimpanzee male aggression, the charging display, involved a mix of running upright, dragging or throwing branches, swaying vegetation, stomping or slapping the ground, and banging on the buttresses of large trees. Displays were often protracted and elaborate, and males were sometimes observed panting after performing them. Initiating aggression is also likely to be intrinsically stressful psychologically. Although high-ranking chimpanzee males can normally expect to win their fights, the widespread use of coalitions means that the outcome of any particular interaction cannot be guaranteed. A male might commence an ostensibly safe attack on a lower-ranked victim, yet end up fleeing from a group of cooperating males. The distinction between physiological and psychological stressors is tenuous, however, as psychosocial factors would not be expected to induce a glucocorticoid response if they did not reliably anticipate genuine metabolic need.

The largest single factor affecting male glucocorticoid levels was the presence of parous estrous females. Males of all ranks showed substantial glucocorticoid increases in the presence of such females. This response was partly driven by aggression, both given and received, as high-ranking males were more likely to be perpetrators, and low-ranking males victims, in reproductive contexts. However, even controlling for involvement in aggression, males showed elevated glucocorticoids in response to parous estrous females. This likely reveals opportunity costs of male mating effort. Males exhibited heightened vigilance in the presence of estrous mothers, closely monitoring their movements and those of male rivals. Dominant males frequently attempted to prevent others from mating, while subordinates sought opportunities to mate surreptitiously. These pursuits interfered with feeding. For example, Georgiev et al. (2014) reported that Kanyawara males of all ranks reduced their feeding time by an average of 25.5% (about one hour per day) during periods when parous estrous females were available. Males did not compensate for lost feeding time by eating higher quality foods, resulting in a tradeoff between mating effort and energy intake.

Instability in the dominance hierarchy was also associated with elevated glucocorticoids in males, but this effect was stronger in higher-ranked individuals, and mediated by aggression. Males who were directly involved in rank changes failed to show disproportionate glucocorticoid increases during periods of instability. It may seem surprising that a high-ranking male was more affected by a reversal at the bottom of the hierarchy than were the males whose ranks actually changed. Young males, however, initiate their careers by challenging individuals at the bottom of the hierarchy, who are often elderly (Goodall, 1986). If successful, they predictably move on to provoke males of higher status. Consequently, any threat to the status quo differentially imperils males at the top of the hierarchy, who have further to fall.

Why were high-ranking males more aggressive than low-ranking males, even in stable dominance hierarchies and non-mating contexts? Muller (2002) proposed that because chimpanzee grouping patterns are so variable, dominant males can never know what political maneuvering has occurred in their absence. Consequently, they must continually be alert to the possibility of shifting coalitions and status challenge, and habitually reassert their dominance through costly displays. This explains the large proportion of chimpanzee aggression that takes place in the context of reunions, when two parties meet after a period of separation (Bygott, 1979; Goodall, 1986). The same dynamic is not expected in species with stable groups, or less pervasive status competition.

Our measure of dietary quality was not associated with male glucocorticoid levels. This finding differs from a previous study in Kanyawara, in which we reported that males showed elevated glucocorticoids during a 4-month period of low food availability in 1998 (Muller and Wrangham, 2004b). This inconsistency is likely explained by the fact that, over that 4-month period, chimpanzees ate ripe fruit in only 20% of feeding observations. That was the lowest level of fruit consumption recorded in 25 years of study (mean = 64%, SD = 15.8, n = 300 months). This suggests that glucocorticoids did rise when fruit availability fell below a critical threshold, but that under most conditions, Kanyawara males adequately compensated for a lack of fruit by falling back on abundant piths and herbs (Wrangham et al., 1996). It is notable that even during the worst period of fruit availability, there was no evidence that chimpanzees rapidly lost condition. For example, out of 926 urine samples collected from community members in 1998, none tested positive for ketones, an indicator of fat mobilization (Muller and Wrangham, 2005). This contrasts with orangutans in Gunung Palung National Park, who routinely tested positive for urinary ketones during lean periods (Knott, 1998).

Finally, glucocorticoids increased with male age, despite older males being less involved in aggression, and less likely to be high ranking. We have previously shown that this increase is probably due to impairments of hypothalamic–pituitary–adrenal regulation that are intrinsic to the aging process (Emery Thompson et al., 2020). Given that both aging and status competition are associated with increased glucocorticoid production, physiological stress may be an important mechanism that constrains a male's ability to maintain high status across the life course.

The fact that acquiring and maintaining high rank entailed chronically elevated glucocorticoids in male chimpanzees is consonant with previous studies from Kanyawara documenting physiological costs to male status striving. For example, dominant males had lower C-peptide levels than subordinates, reflecting less favorable energy balance (Emery Thompson et al., 2009). They also maintained higher testosterone levels than subordinates (Muller and Wrangham, 2004a), indicating elevated energetic costs and potential immunosuppression (Foo et al., 2017; Muehlenbein and Bribiescas 2005; Wingfield et al., 1997).

Were glucocorticoid levels in dominant males high enough to cause reductions in fitness (e.g. Breuner et al., 2008)? Beehner and Bergman (2017: 78) argue that animals in their natural environments are unlikely to experience such reductions, insisting "the starting point for research inquiry should be the assumption that the measured endocrine profile is adaptive." There is no reason to suspect a priori that elevated glucocorticoids in dominant male chimpanzees should reduce fitness, as high-ranking males have repeatedly been shown to sire more offspring than low-ranking males (Boesch et al., 2006; Newton-Fisher et al., 2010; Surbeck et al., 2017; Wroblewski et al., 2009). However, these reproductive gains potentially come at the expense of health and longevity. As previously noted, repeatedly activating the glucocorticoid stress response uses energy that could otherwise be put into somatic maintenance, increasing wear and tear on an organism (Romero et al., 2009; Sapolsky, 1993a). Consequently, in male chimpanzees, glucocorticoids

may serve as a proxy for reproductive investment that trades off against long-term survival (cf. Boonstra et al., 2001). Testosterone is also thought to be involved in this tradeoff, increasing male fitness by steering investment toward mating effort, at the expense of maintenance and longevity (Brooks and Garratt, 2017; Muller, 2017a).

We have previously shown that high rank is a risk factor for respiratory disease (the leading cause of chimpanzee mortality) in older, but not younger, males in Kanyawara (Emery Thompson et al., 2018). This finding suggests a long-term tradeoff between dominance striving and health and longevity. However, direct links among glucocorticoids, testosterone, and health are the subject of ongoing investigation at the site.

Female chimpanzees do not persistently fight over status in the male manner (Foerster et al., 2016), and current evidence suggests that their tradeoffs between reproductive effort and maintenance are less stark. In a previous study at Kanyawara, for example, dominant females maintained lower glucocorticoid levels than subordinates, especially during the energetically challenging period of lactation (Emery Thompson et al., 2010). A new longitudinal analysis found a negligible association between rank and female glucocorticoids, but this only considered rank as a control, and did not explore interactions with factors such as reproductive state (Emery Thompson et al., 2020). Distinct from males, rank was not predictive of respiratory disease in Kanyawara females (Emery Thompson et al., 2018).

Snyder-Mackler et al. (2020) recently proposed that social mammals generally show positive relationships among status, health, and survival. This review was biased toward data on females, however, who are the focus of most demographic research, and often show positive correlations between rank and longevity. Data from a range of vertebrates suggests that high rank in males frequently incurs costs, including elevated parasitism (Habig and Archie, 2015; Habig et al., 2018) and glucocorticoid production (Beehner and Bergman, 2017; Cavigelli and Caruso, 2015; Creel, 2001, 2005). In some species only high-quality males, who can afford such costs, become dominant, resulting in a positive correlation between reproductive effort and survival (Cram et al., 2018; Lloyd et al., 2020; von Holst et al., 1999). In many species, however, males who invest heavily in mating effort show either reduced longevity compared to other males (Beirne et al., 2015; Lemaître et al., 2018; Robinson et al., 2006; Verhulst et al., 2014) or no association between rank and longevity (Creel and Creel, 2002; Hoogland, 1995; McElligott and Hayden, 2000). Thus, the data from Kanyawara may reflect a broader sex difference in the effects of status striving and mating effort on health that deserves further attention.

Acknowledgements

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Appendix A. Supplementary data

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