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ORIGINAL ARTICLE

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Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*)

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Abstract Field studies of endocrine function in a range of social mammals suggest that high dominance rank is commonly associated with elevated glucocorticoid production. This is puzzling, because in stable dominance hierarchies, high status is normally associated with social control and predictability, key predictors of low psychological stress. One solution to this problem may be that high rank is commonly associated with elevated energetic expenditure, leading to increased metabolic stress and glucocorticoid secretion. We conducted behavioural observations and non-invasive hormone sampling of male chimpanzees in Kibale National Park, Uganda, to examine the relationship between cortisol, dominance and stress in wild chimpanzees. Results indicate that male dominance rank positively correlated with urinary cortisol excretion in a stable dominance hierarchy. Cortisol excretion also correlated positively with rates of male aggression. We suggest that the relationship between cortisol and rank in chimpanzees may be driven by energetic factors rather than psychosocial ones. This interpretation is supported by the observation that urinary cortisol levels correlated negatively with food availability. These findings suggest that dominant chimpanzees experience significant metabolic costs that must be set against the presumed reproductive benefits of high rank. Metabolic stress may mediate the relationship between rank and cortisol in other social mammals.

Keywords Chimpanzees · Cortisol · Stress · Dominance · Aggression

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Introduction

The basic physiology of the vertebrate stress response has been well described in both proximate and functional terms (Selye 1956; Chrousos and Gold 1992; Genuth 1993; Sapolsky 1993a). The initial response, mediated by the sympathetic nervous system, involves the secretion of catecholamines (epinephrine and norepinephrine) from the adrenal medulla. These molecules, which facilitate a general state of arousal and vigilance, have wide-ranging physiological effects that include an increase in heart rate, and changes in arteriolar constriction that function to shunt blood toward exercising muscles (Genuth 1993).

The secondary stress response involves an increase in the concentration of circulating glucocorticoids, 21-carbon steroids produced by the adrenal cortex under stimulation of ACTH from the pituitary. This increase occurs within a few minutes of the onset of a stressor. In many birds and rodents the primary glucocorticoid is corticosterone; however, in primates, including chimpanzees and humans, it is cortisol (Nelson 1995).

The most conspicuous of cortisol's physiological effects involve the regulation of metabolism. Cortisol increases the availability of glucose in the bloodstream by promoting the conversion of protein to glucose via hepatic gluconeogenesis (Genuth 1993). At the same time it inhibits the ability of insulin to promote glucose uptake and glycogen synthesis. These effects are understandable from an adaptive perspective: long-term energy storage is curtailed, as energy reserves are mobilized in response to crisis (Sapolsky 1993a).

Although acute rises in cortisol represent an essential, adaptive response to short-term stressors, over time chronically high levels of glucocorticoid secretion can lead to pathology, including gastric ulcers and atherosclerosis (Sapolsky 1993a). Other adverse effects of sustained glucocorticoid exposure include protein breakdown, muscle wasting, and immunosuppression (Genuth 1993; Rabin 1999).

Because the adverse physiological consequences of chronic exposure to high levels of glucocorticoids are so

striking, measurements of these hormones have been used to quantify the costs of specific behavioral strategies and interactions. Particular interest has focused on the relative costs and benefits of social dominance (Creel 2001).

Stress hormones and social dominance

Numerous studies have demonstrated that the magnitude of the cortisol response marshaled by an individual depends upon both the physiological and the psychological aspects of the stressor that induces it (Sapolsky 1993a). Psychological stressors have generally received more attention in the literature, however (e.g. Abbott et al. 2003). Experimental evidence that both unpredictability and loss of control are associated with a heightened stress response led to an early expectation among researchers that in social animals, subordinate individuals should generally maintain higher levels of circulating glucocorticoids than dominants (Creel 2001). Tests of this hypothesis in primates have been performed primarily on captive populations, producing mixed results. For some groups this relationship normally holds true (reviewed in Sapolsky 1992), but in others there is no correlation between cortisol and dominance (squirrel monkeys: Steklis et al. 1986; talapoin monkeys: Martensz et al. 1987; rhesus macaques: Bercovitch and Clarke 1995). To complicate matters, a previous negative correlation between cortisol and rank can disappear when the dominance hierarchy is unstable (squirrel monkeys: Coe et al. 1979; talapoin monkeys: Keverne et al. 1982; macaques: Shively and Kaplan 1984).

Sapolsky (1992) explained the latter observation in terms of a shift in the rank distribution of stress. Specifically, in stable hierarchies, high-rank incurs psychological benefits associated with predictability and control. The result is relatively low basal levels of stress hormones. In unstable hierarchies, however, the social position of high-ranking individuals is threatened, leading to a heightened stress response.

This interpretation is supported by long-term observations of olive baboons in Kenya. Sapolsky (1992) reported that during a period in which the dominance hierarchy was stable, high-ranking baboon males were less aggressive than low-ranking males, and exhibited lower circulating levels of cortisol. During a period of extreme dominance instability, however, high-ranking males were more aggressive and showed higher levels of cortisol than low-ranking males.

Although Sapolsky's baboon data are largely consistent with findings from captivity, they are unusual. Recent field studies suggest that in free-ranging mammals, low levels of circulating glucocorticoids are rarely associated with high dominance rank (Creel 2001; Creel and Sands 2003). For example, in a dozen recent studies conducted on social mammals in the wild, only Sapolsky's unequivocally reported higher levels of glucocorticoids in subordinate individuals. In five populations no significant differences were found between dominants and subordinates (tufted capuchins: Lynch et al. 2002; mountain gorillas: Robbins and Czekala 1997; long-tailed macaques: van Schaik et al. 1991; male dwarf mongooses: Creel et al. 1996; postdispersal spotted hyenas: Goymann et al. 2003). In one population, dominants maintained higher levels of circulating glucocorticoids than some, but not all classes of subordinates (alpine marmots: Arnold and Dittami 1997). And in six populations, dominants consistently maintained higher basal levels of circulating glucocorticoids than subordinates (ring-tailed lemurs: Cavigelli 1999, Cavigelli et al. 2003; Japanese macaques: Barrett et al. 2002; dispersing spotted hyenas: Holekamp and Smale 1998; female dwarf mongooses: Creel et al. 1996; African wild dogs: Creel et al. 1996; wolves: Creel and Sands 2003).

In response to these findings, Creel (2001) has suggested that contrary to the predictions derived from observations in captivity, high levels of cortisol production represent a general cost of social dominance in group-living species. However, the mechanisms that link social dominance with increased cortisol secretion in these species are unknown (Creel and Sands 2003). It seems unlikely that psychological stress could be driving the relationship, because social dominance is not normally associated with loss of predictability and control.

A possible solution to this puzzle may be that social dominance frequently results in increased physiological stress, due to elevated metabolic demands. Cortisol plays a critical role in the stimulation of gluconeogenesis and the mobilization of amino and fatty acids from body stores (Miller and Chrousos 2001). Thus, changes in energetic expenditure and energy balance can affect cortisol production independently of psychological variables. For example, food deprivation increases circulating cortisol levels, such that animals in the wild show clear negative correlations between measures of cortisol excretion and food availability (elephants: Foley et al. 2001; mule deer: Saltz and White 1991). Acute exercise also predictably increases glucocorticoid secretion, in direct proportion to its intensity (Tharp 1975; Perry and Gilmour 1999; Girard and Garland 2002).

In species where aggressive displays are energetically expensive, and rates of aggression differ predictably with rank, agonistic behavior may be an important factor relating dominance to cortisol secretion. Chimpanzees (*Pan troglodytes*) potentially represent such a species, because they engage in frequent aggression, and high-ranking males are significantly more aggressive than lower-ranking individuals (Muller 2002).

In this paper, therefore, we examine the relationship between cortisol excretion, dominance and aggression in wild chimpanzees in an attempt to distinguish the relative contributions of psychological and metabolic factors on cortisol excretion. We begin by testing the hypothesis that cortisol levels in male chimpanzees are affected by energy availability, as assayed through measures of fruit abundance. We then test the hypotheses that male cortisol levels correlate with dominance rank and rates of

agonistic behavior. Finally, we evaluate the stability of the dominance hierarchy during the study period.

Methods

Study site and population

Muller observed chimpanzees from November 1997 through December 1998 at the Kanyawara study site in Kibale National Park, Uganda (0°34′N and 30°21′E). The data presented here are from 1998 only. The Kanyawara chimpanzees occupy a territory of at least 15 km^2 that incorporates areas of primary forest, logged forest, grassland, swamp, exotic softwood plantation, and agriculture (Chapman and Wrangham 1993). Struhsaker (1997) provides a detailed description of the site.

The Kanyawara community were first studied systematically by Isabirye-Basuta (1989) in the early 1980s. They have been studied continuously since September 1987, when Wrangham established the Kibale Chimpanzee Project. During this study all of the males and most of the females were well-habituated to human observers, and could be observed at close range without disturbance. They have never been provisioned.

At the beginning of this study, the Kanyawara community consisted of 50 chimpanzees, including 11 adult males, 15 parous females, 1 subadult male, 2 nulliparous females, 8 juveniles, and 13 infants. Males were considered to have reached adulthood after successfully dominating all females in the community.

Behavioral observations

With the help of long-term field assistants, chimpanzees were followed, whenever possible, from the time that they woke in the morning until the time that they constructed their night nests. All-male and bisexual parties were followed preferentially, in order to facilitate data collection on male aggression.

We employed 40-min group focals to generate rates of aggression (charging displays, chases, and attacks) for individual chimpanzees. Such all-occurrence sampling (Altmann 1974) was possible because the boisterous nature of chimpanzee agonism renders it highly conspicuous to observers. If a party could not be observed for the full 40 min, then the focal follow was abandoned. If a party fissioned during the focal period, then only data from individuals who were observed for the full 40 min were used in rate calculations. In practice such fissioning was rare, occurring in fewer than 8% of the 40-min focals. Muller collected all data taken from January through November. Field assistants from the Kibale Chimpanzee Project collected most of the observations in December; these account for less than 4% of the total.

Behavioral categories followed those of Bygott (1979) and Goodall (1986); these are summarized in Nishida et al. (1999). Charging displays involved exaggerated locomotion, piloerection and branch-shaking. Chases were recorded when an individual pursued a fleeing conspecific, 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. Ad libitum observations of aggression and submission were also recorded by both Muller and field assistants. These were pooled with focal aggression data to assess male dominance rankings, but were not included in estimates of individual aggression rates.

Male dominance ratings are commonly based on the distribution of pant-grunt vocalizations (Bygott 1979; Goodall 1986). Pant-grunt orientation is highly directional, and reliably correlates with multiple measures of dominance (Bygott 1979; Hayaki et al. 1989; Boesch and Boesch-Achermann 2000). In the current study, however, observed pant-grunts were insufficient to distinguish male rank beyond the basic categories of alpha, high, medium, and low (cf. Bygott 1979).

To enhance resolution of male dominance relationships, we applied the Batchelder, Bershad and Simpson (1992, Jameson et al. 1999) model to data on decided agonistic bouts. This model takes into account the number of opponents that an individual has successfully defeated, and the relative success of those opponents in their own agonistic encounters.

Food availability and energy balance

Field assistants in Kanyawara regularly noted at 15-min intervals whether chimpanzees were feeding. If they were, both the species and portion of the plant being consumed were recorded. Fruit availability is estimated indirectly by calculating the total percentage of these feeding observations in which chimpanzees consumed fruit for each month. This measure has previously been shown to correlate with direct estimates of fruit abundance from phenology transects (Wrangham et al. 1996).

Kanyawara chimpanzees eat ripe fruit in proportion to its availability (Wrangham et al. 1998). Because fruit abundance varies temporally, however, 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 should represent times of increased energetic stress.

Urine collection and preservation

First-morning urine samples were regularly collected from chimpanzees, who predictably urinate upon waking. Urine samples were also collected opportunistically throughout the day. When a chimpanzee urinated from a tree, urine was trapped in a disposable plastic bag attached to a 2-m pole. If a bag could not be placed in time, then urine was pipetted from leaves in the ground layer of vegetation. Immediately after collection, the identity of the chimpanzee, the date, and the time of urination were recorded.

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.

One to 24 h after collection (mean: 6.5 h), urine samples were processed and stored in a propane-powered freezer that consistently maintained a temperature between −18° and −23°C. Frozen samples were transported on both ice and dry ice to the Reproductive Ecology Laboratory at Harvard University, where Muller performed all hormone analyses.

Hormone analysis

Steroid levels were quantified by radioimmunoassay according to published protocols (Lipson and Ellison 1989) adapted for use with primate urine. The cortisol assay is based on a four-position tritium competitor (Amersham-Searle) and an antiserum raised against Cortisol-3-0-Carboxymethylether-BSA (ICN Biomedicals no. 07–121016). This antiserum has reported cross-reactivities of 11.4% with 21-desoxycorticosterone, 8.9% with 11-desoxycortisol, and 1.6% with corticosterone; cross-reactions with other naturally occurring steroids are non-significant. Cortisol was assayed directly from unpurified urine diluted 1:10 with distilled water.

Most urinary cortisol is excreted in a conjugated form (Bahr et al. 2000); thus, the values reported here do not reflect absolute levels of free cortisol. However, for these analyses we are interested in relative amounts of cortisol excretion between and within individuals, so measuring absolute values is unnecessary.

Quality control was maintained by monitoring values of urine pools at three different levels. Assay sensitivity, the least amount distinguishable from 0 with 95% confidence, averaged 5,250 pmol/

l. Intra-assay variability (CV) at the 50% binding point of the standard curve was 6%. Inter-assay variability averaged 7.2%, 6.7% and 15.6% for high, medium and low pools (n=16). Linearity of response was verified by assaying serial dilutions of both cortisol standard (predicted vs observed values: r^2=0.99, P<0.0001) and chimpanzee urine (predicted vs observed values: r^2=0.99, P<0.0001).

To correct for variation in urine concentration, steroid levels were indexed to creatinine (Erb 1970; Cook and Beastall 1987). Creatinine is produced when creatine phosphate, a high-energy compound in skeletal muscle, is nonenzymatically dephosphorylated. This is assumed to occur at a relatively constant rate. Creatinine levels were quantified colorimetrically using the Jaffee reaction (Taussky 1954). All cortisol measurements are expressed in pmol/mg creatinine.

Urinary excretion of cortisol in chimpanzees shows a clear diurnal pattern, with highest levels in the early morning, followed by a steady decline throughout the day (Muller and Lipson 2003). We controlled for this effect by analyzing morning samples (those collected before 1000 hours) separately from afternoon samples (those collected after 1000 hours). To preserve independence, when more than one urine sample was collected from a male within a morning or an afternoon, the average of these was taken as the value for that morning or afternoon.

Statistical procedures

Paired comparisons were made with the Agresti-Pendergrast rank-based procedure (Agresti and Pendergrast 1986). This nonparametric test is similar to the standard Wilcoxon signed rank test, but has been shown to exhibit better power properties over a wide range of situations, and particularly when sampling from heavy-tailed distributions (Kepner and Robinson 1988; Wilcox 1997).

Reported correlations are based on Kendall's tau (τ). This rank-based statistic measures the degree to which two variables have a monotonic increasing or decreasing relationship. Because of small sample sizes, P values calculated by the program Statview 4.5 were checked against exact values from statistical tables, following Mundry and Fischer (1998). Statistical tests are two-tailed. Where rank statistics are used, figures report means and standard errors.

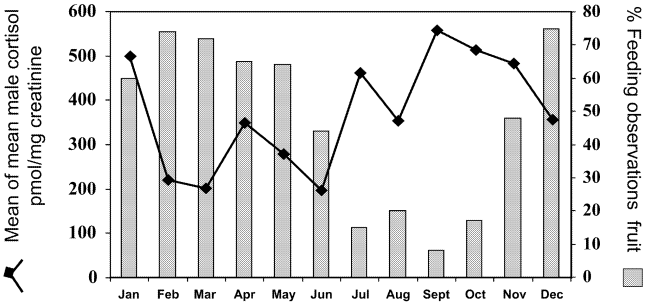

Fig. 1 Mean morning cortisol levels (*line*) and fruit abundance (*bars*) by month. Morning cortisol levels were negatively correlated with the percentage of monthly feeding points in which chimpanzees were observed eating fruit

Table 1 Fruit availability by month: Kanyawara 1998. "Feeding observations" indicates the total number of 15-min points in which chimpanzees were observed feeding each month. Subsequent columns show the percentage of feeding records in which drupes, figs, or drupes plus figs ("fruits") were consumed

Month	Feeding observations	% With drupes eaten	% With figs eaten	% With fruit eaten
January	640	47	13	60
February	833	0	74	74
March	832	0	72	72
April	809	7	57	65
May	551	26	38	64
June	1001	4	39	44
July	433	0	15	15
August	336	0	20	20
September	272	0	8	8
October	573	0	17	17
November	496	10	38	48
December	511	72	3	75

Results

Fruit availability and cortisol

Distinct periods of high and low fruit abundance were apparent during the 12 months of this study (Fig. 1). Table 1 shows, for each month, the percentage of feeding observations in which chimpanzees consumed fruit. July through October represented a 4-month period of low fruit availability, with fewer than 20% of monthly feeding observations including figs or drupes. February through May represented a comparable time period of higher fruit availability, with 60–80% of monthly feeding observations including figs or drupes.

To examine whether variation in male cortisol levels was related to changes in food availability, we used morning urine samples to calculate, for each month, an individual mean cortisol level for each chimpanzee male. We then took the average of these individual means to get a "mean of individual means" for each month. These means of individual mean cortisol levels were negatively correlated with our monthly measure of fruit abundance (Kendall correlation: τ=–0.49, P=0.028, n=12). A similar pattern emerged when mean monthly morning cortisol concentrations from the most frequently sampled male (LK) were analyzed separately (τ=–0.61, P=0.006, n=12).

Sample coverage was insufficient to repeat this monthly analysis with afternoon cortisol measures. However, paired comparisons of male cortisol concentrations between the low fruit (July–October) and high fruit (February–May) periods suggest that food availability affected cortisol excretion in morning samples only. Mean morning cortisol concentrations in the low fruit period (496±32 pmol/mg creatinine) were significantly higher than in the high fruit period (315±24 pmol/mg creatinine) (Agresti-Pendergrast procedure: F=29.84, P<0.001, n=10 males, Fig. 2). The low P value reflects the fact that this effect was observed in all of the males. There was not a significant difference in afternoon cortisol concentrations between the low fruit (210±22 pmol/mg creatinine) and high fruit periods (215±48 pmol/mg creatinine) (Agresti-Pendergrast procedure: F=0.991, P=0.345, n=10 males).

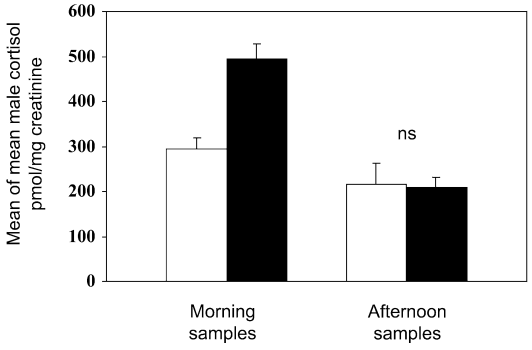

Fig. 2 Mean male cortisol levels during periods of high (*open bars*) and low (*solid bars*) fruit abundance. Cortisol levels were significantly higher during the period of low food availability for morning, but not afternoon, samples

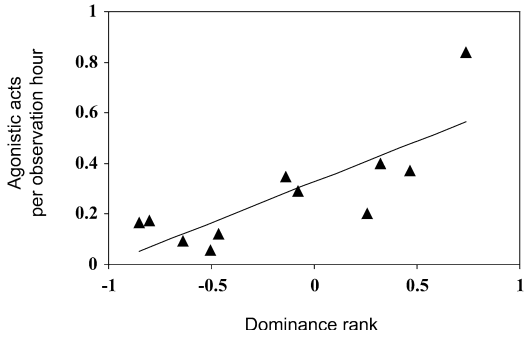

Fig. 3 Male dominance rank and frequency of aggression. Rates of aggression (displays, chases, and attacks) were positively correlated with male dominance rank

Dominance and cortisol

Table 2 shows the distribution of decided agonistic encounters among dyads. These data were used to generate a probabilistic dominance rank for each male. Males received scaled values between −1 and 1, with 1 representing high rank (Table 3). The distance between the scaled values indicates a difference in the magnitude of dominance (i.e. males with similar values are more difficult to distinguish in rank than those further apart). Across the adult males, dominance rankings were positively and significantly correlated with rates of aggression (Kendall correlation: τ=0.60, n=11, P=0.010, Fig. 3).

Throughout this study, the male dominance hierarchy appeared to be stable. Table 2 shows the distribution of 89 observed pant-grunts among the adult males. Fifty-seven of these were directed toward the alpha, MS. No reversals were recorded in any of the pant-grunt interactions (i.e. within all possible dyads, pant-grunts were given by only one of the males). Only 3 out of 107 decided dyadic agonistic encounters represented reversals, a rate of 2.8%. (11 additional dyadic encounters were excluded from Table 2 because they were scored as "undecided." These generally involved one male charging another male, but being ignored. Seven of these interactions involved low-ranking males; only four involved top-ranking males.)

Across the adult males, mean afternoon cortisol levels were positively and significantly correlated with dominance rank during both the low-food season (τ=0.59, P=0.012, n=9) and the high-food season (τ=0.51, P=0.028, n=9). A similar correlation is evident between dominance rank and mean male cortisol levels from all afternoon samples in 1998 (τ=0.46, n=11, P=0.052, Table 3). Mean morning cortisol levels, on the other hand, were not significantly correlated with dominance rank during any of these periods (low-food season: τ=−0.11, P=0.65, n=9; high-food season: τ=0.31, P=0.19, n=9; all 1998 samples: τ=0.35, n=11, P=0.14, Table 3).

Table 3 Mean morning and afternoon cortisol values for 11 adult males. Sample sizes are the number of daily cortisol values, followed by the total number of urine samples used to calculate those values (in *parentheses*). Includes all samples from 1998. Cortisol is expressed in *pmol/mg* creatinine

Individual		Morning samples		Afternoon samples	
Male	Rank	Mean *C*	*n*	Mean *C*	*n*
MS	.739	568	36(38)	230	15(16)
AJ	.465	427	28(30)	244	7(8)
TU	.320	455	17(17)	200	5(5)
BB	.258	431	13(13)	277	6(7)
SL	−.078	281	6(6)	237	4(5)
LB	−.138	316	36(47)	150	26(30)
BF	−.467	450	13(14)	232	8(8)
ST	−.505	389	38(40)	120	8(10)
SY	−.641	337	31(36)	121	18(21)
YB	−.800	402	41(47)	197	18(22)
LK	−.853	381	46(56)	147	22(30)

Table 2 Dominance relationships among adult males at Kanyawara. Entries are the number of times that the row male pant-grunted to/lost a dyadic agonistic bout with the column male. Data are from focal follows and ad libitum observations in 1998

	MS	AJ	BB	TU	LB	SL	BF	ST	YB	SY	LK
MS	*	0/1		0/1							
AJ	6/5	*									
BB	4/3	0/2	*								
TU	4/2	0/1	0/1	*							
LB	13/11	1/4	1/2	2/1	*	0/1					
SL	12/3	0/0	0/0	1/2	0/2	*					
BF	1/2	0/1	0/0	0/0	0/0	0/3	*				
ST	1/3	0/4	1/4	0/2	0/2	0/0	0/0	*			
YB	0/1	4/1	0/1	0/4	0/2	0/0	0/1	1/0	*		
SY	7/4	4/6	1/2	1/1	2/2	1/2	0/1	0/0	2/0	*	
LK	9/4	2/3	1/2	2/0	1/2	1/1	0/0	1/3	2/0	0/1	*

Table 4 Rates of male aggression during periods of high and low fruit availability. Includes data from adult males for whom at least 25 observation hours were available during each season. (Male BF disappeared part-way through the study, so is represented only during the high-food season.) Data from parties containing fewer than two adult males have been excluded

ID	All 1998		February–May 1998 (high food season)		July–October 1998 (low food season)	
	Observation hours	Aggression rate	Observation hours	Aggression rate	Observation hours	Aggression rate
MS	183	0.838	51	0.994	65	0.765
AJ	163	0.369	55	0.457	57	0.353
TU	115	0.399	33	0.337	47	0.214
BB	109	0.201	42	0.214	44	0.136
SL	51	0.292	11	*	12	*
LB	183	0.345	89	0.325	43	0.462
BF	33	*	25	0.203	2	*
ST	145	0.055	54	0.000	60	0.083
SY	119	0.093	62	0.065	37	0.191
YB	162	0.173	64	0.156	50	0.142
LK	167	0.167	79	0.164	44	0.114

Aggression and cortisol

Table 4 shows individual rates of male aggression (charging displays, chases, and attacks) at Kanyawara in 1998. Across the adult males, mean afternoon cortisol levels were positively and significantly correlated with individual rates of aggression during the high-food season (Kendall correlation: τ=0.53, n=11, P=0.03); in the low-food season this correlation was not significant (τ=0.48, n=9, P=0.07). When individual rates of aggression were calculated for all of 1998, these were positively and significantly correlated with mean male cortisol levels from all afternoon samples in the same year (τ=0.51, P=0.04, n=10).

Mean morning cortisol levels, on the other hand, were not significantly correlated with rates of aggression during the low-food season (τ=0.11, n=9, P=0.68) or the high-food season (τ=0.2, n=11, P=0.48). When individual rates of aggression were calculated for all of 1998, these were not significantly correlated with mean male cortisol levels from all morning samples in the same year (τ=0.42, P=0.09, n=10).

Discussion

The relationship between urinary cortisol excretion and dominance rank in chimpanzee males differed by time of day. For morning samples, the correlation was weak and statistically insignificant, whereas for afternoon samples, the correlation was positive and significant. Stronger correlations of behavioral measures with evening than with morning steroid levels appear to be widespread in chimpanzees and humans, in part because morning levels reflect physiology during sleep, whereas evening levels reflect waking activity patterns and the cumulative outcomes of diurnal social interactions (e.g. Worthman and Konner 1987; Berg and Wynne-Edwards 2001; Book et al. 2001; Muller and Wrangham 2003).

Because of the lag time between steroid production and excretion, urinary cortisol levels in chimpanzees reflect endocrine status several hours (2–4) prior to sampling (Whitten et al. 1998; Bahr et al. 2000). Morning levels are thus expected to reflect overnight glucose mobilization. It is therefore not surprising that our proxy measure of energy availability (% feeding observations containing fruit) correlated negatively with cortisol levels in morning samples. Foley et al. (2001) reported a similar negative association between rainfall (a proxy for food availability) and fecal cortisol concentrations in African elephants.

The positive correlation between dominance rank and urinary cortisol reported here is consistent with results from field studies conducted on a range of social mammals (Creel 2001). In theory high-ranking chimpanzees could have exhibited increased levels of urinary cortisol excretion because they experienced higher levels of metabolic stress, higher levels of psychosocial stress, or both.

The hypothesis that higher-ranked males in this study experienced increased levels of psychosocial stress received little support. Psychological stress is typically associated with loss of predictability and control (Sapolsky 1993a; Creel 2001). Thus the normal expectation is that high-ranking males should exhibit increased cortisol in unstable social hierarchies, when their dominance is threatened (Sapolsky 1993b). However the dominance hierarchy at Kanyawara was stable throughout the study period. There were no rank reversals, and the rate of reversals in decided agonistic bouts was less than 3%.

The alternative hypothesis, that high-ranking males exhibited increased rates of cortisol production because they were more frequently mobilizing energy stores to meet elevated metabolic demands, cannot be ruled out. Aggression represents a metabolic demand that may be salient. High-ranking males exhibited aggression more frequently than low-ranking males, and rates of aggression were correlated with afternoon cortisol excretion.

Although detailed data on the specific energetic costs of aggression in male chimpanzees are lacking, these are not likely to be trivial. The most frequent form of aggression, the charging display, involves running upright, dragging or throwing branches, stomping the ground, and vocalizing. Such displays can be protracted

and elaborate, and males are often observed breathing heavily after performing them. In the present study the alpha male regularly started his day by vigorously charging underneath the trees where rival males were sleeping, then climbing up to chase them from their night nests. These displays frequently persisted for several minutes, and were repeated after intervals of rest.

The possibility remains that engaging in aggression is psychologically stressful in ways that we did not detect, and that this partially accounts for the correlation between aggression and cortisol production observed here. However, this seems unlikely when the key criteria of predictability and control are considered. High-ranking males won almost all (>97%) of the agonistic interactions that they initiated. Thus, the outcome of aggressive behavior was highly predictable, a pattern that is typical of stable chimpanzee hierarchies.

It is also possible that the observed dominance hierarchy was unstable in ways that we were unable to detect, and that this led to increased psychological stress in high-ranking males. Previously Muller (2002) has suggested that chimpanzee dominance hierarchies may be perpetually unstable in comparison to those of baboons, due to the fission-fusion nature of chimpanzee social organization. Specifically, because chimpanzee party composition is highly unstable, a top-ranking male can never know what political maneuvering has occurred in his absence. He must continually be alert to the possibility of shifting coalitions and status challenge, and be prepared to habitually reassert his dominance. Ongoing hormonal monitoring of chimpanzees in both Kibale and Gombe National Park (Tanzania) will allow us to further address this issue, by comparing the dominance styles of high-ranking males. The data presented here, however, suggest that metabolic influences on stress should receive increased attention in studies examining the relationship between social status and endocrine function.

Because animals in the wild generally have suboptimal access to energy, they may be expected to frequently exhibit changes in cortisol production related to changes in energetic status, and pure metabolic stress may commonly account for a high proportion of the variation in glucocorticoid secretion. Captive animals exhibit much less variability in both condition and energetic expenditure. Thus, in captive populations psychosocial stress should account for a greater proportion of glucocorticoid variation. This might also be true of wild populations living under particularly favorable energetic conditions, such as baboons that have access to human food waste from tourist lodges (e.g. Kemnitz et al. 2002). Creel et al. (1996) note that other factors in captivity could exacerbate this effect; for example, artificial spatial constraints make it more difficult for low-ranking individuals to avoid dominants, thus increasing the intensity of psychosocial stress.

It is not currently clear why dominant individuals in a number of social carnivores exhibit increased rates of glucocorticoid secretion compared to subordinates (Creel and Sands 2003). Here aggression is not always a salient factor. Among wild dogs, for example, dominant individuals are not involved in aggressive interactions more frequently than subordinates, except during the mating season. Dominants maintain higher basal levels of circulating glucocorticoids throughout the year, however (Creel et al. 1996). And in free-ranging wolves dominant individuals are no more aggressive than subordinates, yet they also maintain higher levels of glucocorticoids throughout the year (Creel and Sands 2003). We believe that a fruitful approach to this problem may be to examine whether dominants and subordinates show predictable variation in energy mobilization due to differences in activity patterns. These could potentially include longer day ranges, increased hunting effort, or higher rates of territorial behavior among dominants. Such rank differences in energetic expenditure might also account for the correlation between age and glucocorticoid secretion in these species (Creel and Sands 2003).

Although aggression represents a potentially significant metabolic demand on male chimpanzees, other variables are likely to play a role in mediating glucocorticoid production. Future studies will evaluate additional factors that may differ between high and low-ranking males, including day range. In the meantime it appears that increased levels of glucocorticoid production represent a cost to male chimpanzees that must be set against the presumed reproductive benefits of high rank.

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